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# The Cyathaspididae

## A Family of Silurian and Devonian Jawless Vertebrates

### INTRODUCTION

The Cyathaspididae, a family of the Order Heterostraci, is the earliest group of vertebrates that is known from more than fragmentary remains. Its range extends from the Middle Silurian through the Early Devonian, and it occurs in North America, Europe, and Asia. As interpreted in this work, the family includes 63 named species grouped in 19 genera. The first cyathaspids were described in 1856 and were included with *Pteraspis* in the Pteraspididae. It was not until relatively recently that they were recognized as a distinct higher category. Jaekel in 1911 (p. 33) subdivided his order Heterostraci into the suborders Palaeaspidi and Pteraspidi, the former corresponding to the Cyathaspididae of this paper. This usage was not followed until Kiaer in 1932 presented the first broad and comprehensive classification of this group. Kiaer's suborder Cyathaspida corresponds to the family Cyathaspididae of this paper, while his families (Poraspidae, Palaeaspidae, Dinaspidae, Anglaspidae, Ctenaspidae, Cyathaspidae, and Tolypaspidae) correspond approximately to the subfamilies used in this paper. It was in Kiaer's paper that the name Cyathaspididae (in the form Cyathaspidae) was first employed.

The history of the study of the Heterostraci, and in particular of the Cyathaspididae, was reviewed in considerable detail by Kiaer and Heintz in 1935 (pp. 19–39). Since that time a number of works have dealt with this family. A general account has been presented by Heintz (1938, pp. 50–54). Classification has been discussed by Flower and Wayland-Smith (1952, pp. 356–372), Denison (1953, pp. 291–293), and Tarlo (1962a, pp. 254–258). General morphological studies have been made by Watson (1954, pp. 9–13), Stensiö (1958, pp. 294–321; 336–401), and Heintz (1962, p. 24). The lateral line system has been considered by Säve-Söderbergh (1941, pp. 530–539), Holmgren (1942, pp. 8–13) and Stensiö (1958, pp. 401–407), and the histology of the shield has been described by Bystrow (1955, pp. 480–491; 1959, pp. 60–62) and Gross (1961, pp. 90–96; 108–109).

The evolution of Heterostraci has been discussed by White (1935, pp. 434–436), Obruchev (1945, pp. 263–266), Stensiö (1958, pp. 294–321), and Tarlo (1962a, pp. 268–277, 1962b). The ecology has been considered by Denison (1956, pp. 416–417). New Cyathaspididae from the United States have been described by Bryant (1935, pp. 112–119), Flower and Wayland-Smith (1952, pp. 372–385), Denison (1953, pp. 294–304; 1960, pp. 555–567), and Beerbower and Hait (1959, pp. 201–203). New cyathaspids from Canada have been described by Denison (1963, pp. 108–132), from England by Wills (1935, pp. 428–435), from Russia by Obruchev (1938, pp. 36–38; 1958, p. 43) and Bystrow (1959, pp. 59–62), and from China by P'an (1962, pp. 407–408).

Much of the material upon which this work is based is in the collections of Chicago Natural History Museum, designated by the initials "CNHM" before specimen and slide numbers. In addition I have been able to borrow for study North American material from a number of institutions. I wish to express my appreciation to the following: Dr. Glenn L. Jepsen and Dr. Donald Baird of the Department of Geology, Princeton University, for the loan of material from New Jersey, New York, Pennsylvania, and the Yukon; Dr. Alfred S. Romer and Miss Nelda Wright of the Museum of Comparative Zoology at Harvard University for the loan of the type material from the Vernon Shale of New York; Mr. Clinton F. Kilfoyle of the New York State Museum for the loan of specimens from the Silurian of southeastern New York; Dr. Gordon Edmund of the Royal Ontario Museum for the loan of the type of *Diplaspis acadica*; the California Standard Company of Edmonton, Alberta, and particularly Dr. Alfred Lenz, for the gift of specimens from northern Yukon, northwestern British Columbia and Northwest Territories, Canada (the types and representative specimens have been deposited in the National Museum of Canada, the rest retained in the collection of Chicago Natural History Museum); Dr. J. R. Beerbower of Lafayette College for the gift of specimens from the Silurian of Pennsylvania and Maryland; Dr. Shelton P. Applegate of the Los Angeles County Museum for the loan of Claypole's syntypic material of *Americaspis americana;* and Dr. W. P. Leutze of New Orleans for the gift of specimens from the Silurian of Maryland and West Virginia.

In 1953–54, thanks to a grant from the John Simon Guggenheim Foundation, I had the opportunity to study much of the European material at the Paleontologisk Museum in Oslo, Naturhistoriska Riksmuseet in Stockholm, and the British Museum (Natural History) and Geological Survey and Museum in London. I wish particularly to thank Dr. Anatol Heintz for permission to cast important specimens in the collections at Oslo, and for providing in an exchange

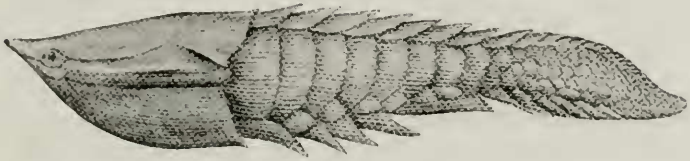

FIG. 90. Restoration of *Anglaspis heintzi* (from Kiaer, 1932); lateral view (× about 3/2).

Spitsbergen specimens that have been extremely useful. I wish also to thank Dr. Tor Ørvig of Stockholm for the loan of the type of *Seretaspis zychi*, and Dr. Errol I. White of London for help in obtaining copies of hard-to-find literature.

The following figures have been drawn, many from my original sketches, by Dr. Tibor Perenyi, staff artist at Chicago Natural History Museum: figures 91, 93, 97–102, 103,A, 113, 127, 130, 132, 155 and 161.

## MORPHOLOGY

The mineralized skeleton of the Cyathaspididae is entirely dermal, and consists of a shield or carapace covering the anterior part of the body, and of scales covering the posterior part and tail (fig. 90). The shield (fig. 91) consists of relatively few elements, of which the most important are the dorsal shield, the ventral shield, and the paired branchial plates.

### Dorsal Shield

The dorsal shield (rostrodorsal disc of Stensiö, 1958, p. 295) is elongate and variously arched. It ranges in length in known cyathaspids from 20 mm. in *Homalaspidella nitida* and *Anglaspis insignis* to 110 mm. in *Allocryptaspis utahensis*. Its anterior border may be smoothly convex (figs. 109, 113, 146, 149, *ro*), or may have a rounded median rostral process (figs. 117,A, 123,C, 135,B, *mrp*). The rostral border is folded under to form the maxillary brim (maxillary plate of Kiaer, 1928, p. 123; maxillar brim of Kiaer and Heintz, 1935, p. 44; subrostral lamella of Stensiö, 1958, p. 352), which forms the dorsal or anterior border of the mouth (figs. 91,B, 92, 105, 132, *mxb*). Stensiö (1958, fig. 194) shows in *Poraspis* a postrostral ascending lamella extending backward and upward from the maxillary brim, but this is not present in sections of this genus figured by Kiaer and Heintz (1935, pl. 38). The orbits notch the sides of the anterior part of the shield, and are usually delimited anteriorly by marked preorbital processes (figs. 91, 113, 123, *pop*). The dorsal shield is generally curved down at the sides to meet the branchial plates, but may develop distinct, laterally directed brims (*Cyathaspis, Listraspis* (fig. 132, *lbr*), *Anglaspis, Ctenaspis*). In *Ariaspis* (fig. 149, *lbr*) there are small but distinct, downwardly directed lateral laminae. There is a single external branchial opening on each side, and its position is usually indicated on the dorsal shield by the downward flexure of the margin to form the postbranchial lobe (fig. 91, *pbl*). The postbranchial lobes are absent in *Ariaspis* and *Ctenaspis,* and are small or absent in *Anglaspis.* They have an abruptly truncate anterior edge in the Irregulareaspidinae and *Pionaspis;* in the latter (figs. 127, 130) this edge is turned inward to form the posterior boundary of the external branchial opening. The postero-lateral corners of the dorsal shield are usually rounded, but are pointed in *Anglaspis, Listraspis* (fig. 132) and *Ariaspis* (fig. 148). The posterior edge of the shield is usually convex, and may have a median lobe or point. In only one cyathaspid, *Ariaspis* (fig. 148, *ms*), is there a ridge scale incorporated to form a median dorsal spine. *Cyathaspis, Listraspis,* and *Ctenaspis* have a median crest on the posterior part of the dorsal shield.

The dorsal shield appears on its inner surface to be a single element, but externally there may be apparent subdivision into areas distinguished by differences in the superficial ridge pattern, and sometimes by what appear to be sutures. These areas are called epitega, a name introduced by Stensiö (1958, p. 297). The anterior area is the rostral epitegum (fig. 112,A, *rep*). Paired lateral epitega (fig. 112,A, *lep*) (marginal prebranchial epitega of Stensiö, 1958, p. 297) extend along the sides from in front of the orbits posteriorly as far as the external branchial openings, or beyond in *Listraspis.* The large central area of the shield, the central epitegum (fig. 112,A,

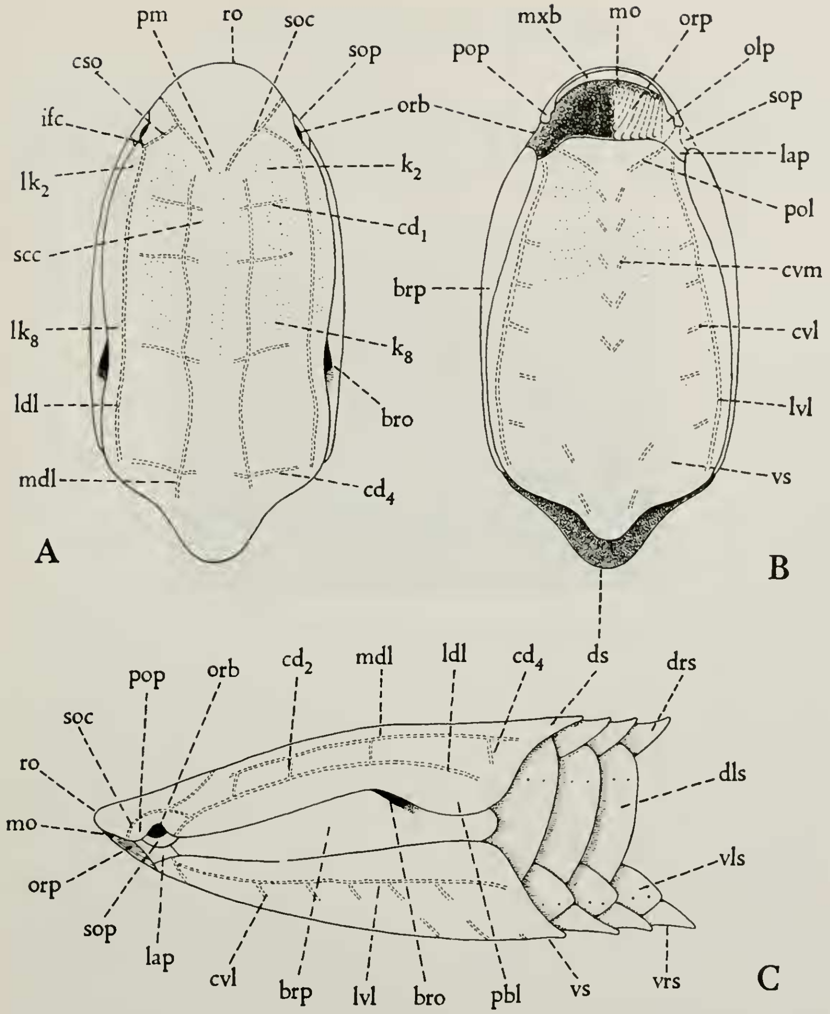

FIG. 91. Shield and anterior scales of *Poraspis* (after Kiaer and Heintz, 1935, with modifications). A, dorsal view; B, ventral view; C, lateral view.

*bro*, branchial opening; *brp*, branchial plate; $cd_{1-4}$, first to fourth dorsal transverse sensory commissures; *cso*, transverse supraorbital sensory commissure; *cvl*, lateral ventral transverse sensory commissure; *cvm*, medial ventral transverse sensory commissure; *dls*, dorso-lateral scale; *drs*, median dorsal scale; *ds*, dorsal shield; *ifc*, infraorbital sensory canal; $k_{2-8}$, positions of inner impressions of gill pouches, numbered according to the theory of Stensiö; *lap*, lateral plate; *ldl*, lateral dorsal sensory canal; $lk_{2-8}$, position of inner impressions of extrabranchial atria or exhalant ducts; *lvl*, lateral ventral sensory canal; *mdl*, medial dorsal sensory canal; *mo*, mouth; *mxb*, maxillary brim; *olp*, oral-lateral plate; *orb*, orbit; *orp*, oral plate; *pbl*, postbranchial lobe; *pm*, pineal macula; *pol*, postoral sensory canal; *pop*, preorbital process; *ro*, rostrum; *scc*, semicircular canal; *soc*, supraorbital sensory canal; *sop*, suborbital plate; *vls*, ventro-lateral scale; *vrs*, median ventral scale; *vs*, ventral shield.

*cep*), lies between the lateral epitega, and extends from the rostral epitegum to the posterior border. A pineal macula (figs. 91, 124, *pm*) is usually marked by its ridge pattern and a prominence, but there is no foramen. There is sometimes a distinct postrostral field (fig. 112,A, *prf*) (Stensiö, 1958, pp. 299-300 = pineal triangle of Denison, 1963), including the pineal macula posteriorly, and expanding forward to its meeting with the rostral epitegum; this may not be a distinct epitegum, but only a part of the central epitegum that is demarked by the supraorbital sensory canals.

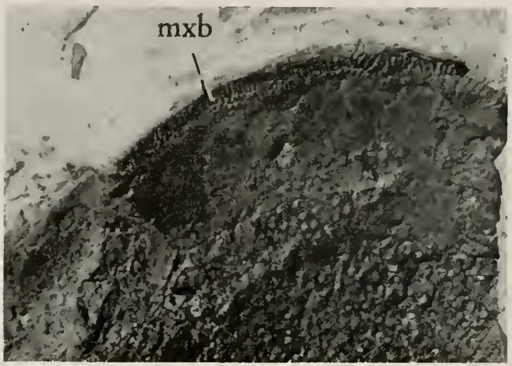

FIG. 92. *Allocryptaspis laticostata*, CNHM, PF 1811; ventral side of incomplete rostrum, showing maxillary brim, *mxb* (× 3).

Except in *Ctenaspis*, the surface of the shield is covered with dentine ridges, sometimes elongate, and at other times broken into short lengths or denticles. The ridges are arranged according to a pattern that is taxonomically important in general, though it may be variable in detail. In some genera the ridges are arranged in scale-like areas that presumably represent fused scales of an ancestral condition. The fineness of the ridges is also of taxonomic importance, and has been represented as the number of ridges per millimeter. This is usually measured in the central part of the dorsal shield; near the lateral borders the ridges are usually finer, and on the ventral shield they are usually slightly coarser. In a few cyathaspids there are coarser and higher ridges separated by a number of lower and finer ridges. Dentine ridges also cover the maxillary brim, usually arranged parallel to the anterior edge, though they have an anteroposterior arrangement in *Allocryptaspis laticostata* (fig. 92). The crests of the ridges may be flat, or roundly or angularly convex, and tend to be higher and sharper near the lateral borders, especially over the orbits and branchial openings. Between the ridges are narrow intercostal grooves that are comparable to the canals of the pore-canal system of some other fishes (Gross, 1956, p. 135).

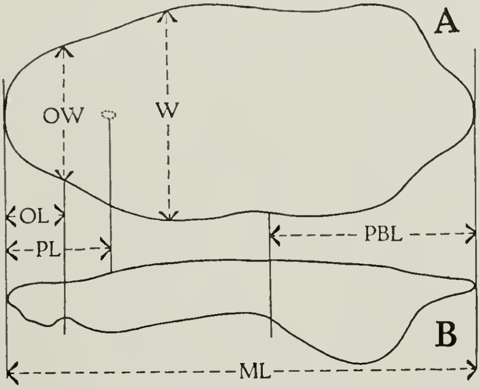

FIG. 93. Dorsal shield of a cyathaspid, showing measurements employed. A, dorsal view, and B, lateral view.

*ML*, median length; *OL*, orbital length; *OW*, orbital width; *PBL*, postbranchial length; *PL*, pineal length; *W*, maximum width.

The following measurements (fig. 93) and ratios have been used for the dorsal shield:

Median length (or length)

Maximum width (or width)

Orbital width (or width at orbital notches)

Orbital length (or median length from anterior border to a line between the orbital notches)

Pineal length (or median length from anterior border to the center of the pineal macula)

Postbranchial length (or median length from posterior border to a line between the external branchial openings)

$$\text{Width ratio} = \frac{\text{maximum width}}{\text{median length}}$$ (breadth-length index of Kiaer and Heintz, 1935, p. 46)

$$\text{Orbital width ratio} = \frac{\text{orbital width}}{\text{median length}}$$

$$\text{Orbital ratio} = \frac{\text{orbital length}}{\text{median length}}$$ (rostral index of Kiaer and Heintz, 1935, p. 46)

$$\text{Pineal ratio} = \frac{\text{pineal length}}{\text{median length}}$$

$$\text{Postbranchial ratio} = \frac{\text{postbranchial length}}{\text{median length}}$$

### Ventral Shield

The ventral shield (fig. 91, *vs*) has relatively few diagnostic characters compared to the dorsal shield. It extends from the posterior borders of the oral or postoral plates to the posterior end of the carapace, and covers the area between the branchial plates. Anteriorly it is relatively flat, but posteriorly it is deeply vaulted, usually more so than the dorsal shield. Its anterior border is most commonly slightly concave, but in some genera it is transverse or slightly convex; in *Allocryptaspis laticostata* (figs. 152,C) it is notched for the reception of postoral plates. At its antero-lateral corners there may be shallow notches for the reception of lateral plates. The lateral edges abut against or are slightly overlapped by the ventral edges of the branchial plates (Kiaer and Heintz, 1935, figs. 53–54). In *Ctenaspis* the lateral margins are formed as brims. The postero-lateral corners are usually rounded, but are pointed in *Ctenaspis*. The posterior edge is usually similar to that of the dorsal shield, and may be transverse or convex, with or without a median lobe or point. In *Allocryptaspis* (fig. 152,B) the dorsal and ventral shields meet behind the branchial openings; in other cyathaspids (fig. 91,C) they are separated here by the branchial plates. *Allocryptaspis* is exceptional in lacking free branchial plates and in having the branchial openings notch the ventral as well as the dorsal shield. This may be true in *Ctenaspis* also. Most of the dentine ridge pattern is either longitudinal or elliptical on the ventral shield. Anteriorly the longitudinal ridges commonly radiate fan-wise toward the antero-lateral corners. In some cases, notably in *Cyathaspis* (fig. 110,B), there are bands of ridges parallel to the anterior edge, and to the anterior part of each lateral edge. Stensiö (1958, p. 308) distinguished these and other areas as "hypotega," comparable to the epitega of the dorsal shield. There is reason to doubt, however, that these "hypotega" have any great significance as structural or growth units, as is pointed out below (p. 460). The only measurements made on the ventral shield, besides dentine ridges per millimeter, are median length and maximum width. The only ratio used is the width ratio, or maximum width/median length.

### Branchial Plates

These have been recognized in less than half of the genera of Cyathaspididae. They are elongate, slender plates (fig. 91, *brp*) that normally articulate with the lateral edges of the ventral shield, and of the dorsal shield behind the orbits. They are curved antero-posteriorly to follow the curvature of the dorsal and ventral shields, and are arched dorso-ventrally, or have a sharp lateral angulation in *Anglaspis*. Their structure is best known in *Poraspis*, thanks to the complete description and excellent figures of Kiaer and Heintz (1935, pp. 46, 118–125, figs. 51–54, pl. 33, figs. 4–6). In this genus the attachment to the dorsal shield is loose and separated by a skin fold anterior to the branchial opening; the attachment behind the branchial opening and to the ventral shield is partially overlapping and presumably firmer. The dorsal border of the branchial plate of *Poraspis* (fig. 91, *brp*) has a well-marked notch that forms the lower border of the branchial opening. The notch is less distinct in *Homalaspidella* (Kiaer and Heintz, 1935, pl. 30, fig. 1), *Archegonaspis* (Heintz, 1933, figs. 1–3), *Vernonaspis* (Ruedemann, 1916, pl. 32, fig. 7), and *Anglaspis* (Wills, 1935, pl. 1, figs. 9–11). The anterior margin in *Poraspis, Anglaspis,* and *Listraspis* is divided by an angulation into two parts, of which the upper is an overlapping margin for the suborbital plate, while the lower presumably articulates with a lateral plate. The dentine ridges are predominantly longitudinal, especially on the dorsal part of the plate, but may be strongly diagonal on the ventral part.

In three genera of cyathaspids the branchial plates are fused or probably fused to the dorsal shield. In *Listraspis* (fig. 132) each of them is attached to the medial edge of the ventral surface of the lateral brim, and the branchial opening is preserved as a slit between it and the brim in approximately its usual position. In *Allocryptaspis* (fig. 153, *ll*) the presumed equivalents of the branchial plates form ventro-mesially directed laminae on the sides of the dorsal shield, entirely anterior to the branchial openings. Similar laminae in *Ctenaspis* (fig. 155, *vll*) may represent the branchial plates.

### Suborbital Plates

Articulated cyathaspids that preserve the smaller plates and scales in their normal position are extremely rare. Two specimens of *Anglaspis heintzi* (Paleontologisk Museum, Oslo, D 382, 384) furnished the information for Kiaer's (1932, fig. 11) well-known reconstruction, but they have not been completely described. An articulated but imperfect specimen of *Irregulareaspis hoeli* (Kiaer, 1932, pl. 5) preserves the suborbital plate, but not the plates of the mouth region. The type of *Archegonaspis integra* (Heintz, 1933, fig. 2) is articulated, but the small anterior plates, if preserved, have not been figured or described.

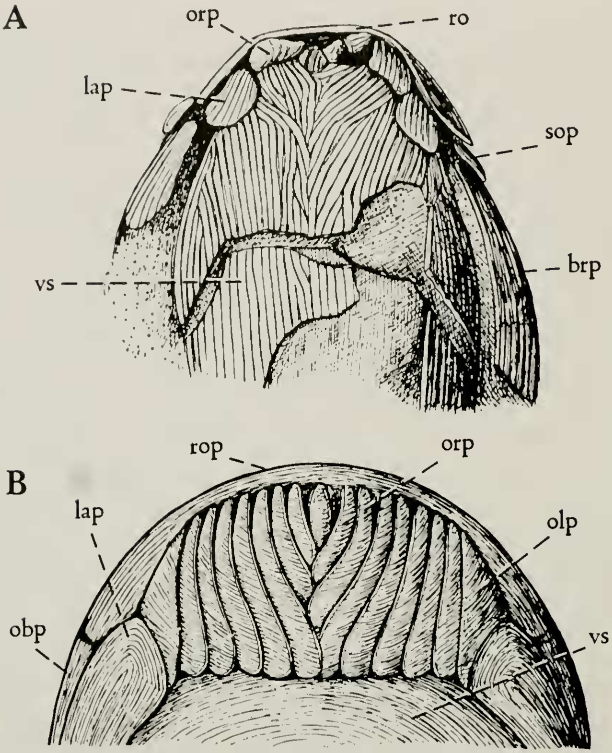

Fig. 94. A, *Anglaspis heintzi;* ventral view of anterior part of articulated specimen, Paleontologisk Museum, Oslo, D 384 (× 3). B, *Protopteraspis vogti;* reconstruction of ventral side of anterior part of shield (× 4). (Both from Heintz, 1962.)

*brp*, branchial plate; *lap*, lateral plate; *obp*, orbital plate; *olp*, oral-lateral plate; *orp*, oral plate; *ro*, rostrum; *rop*, rostral plate; *sop*, suborbital plate; *vs*, ventral shield.

Kiaer's reconstruction (fig. 90) shows the suborbital of *Anglaspis* to be a small, curved plate forming the whole lower border of the orbit. Anteriorly it abuts against the preorbital process, and posteriorly it meets the upper facet of the anterior edge of the branchial plate, as well as the postorbital border of the dorsal shield. The suborbital plate of *Irregulareaspis* (Kiaer, 1932, pl. 5, fig. 2) is similar but relatively larger. In *Listraspis* (fig. 132, *sop*) the suborbital plate is fused to the dorsal shield, and forms the part of the ventral surface of the lateral brim that lies between the branchial plate and the equivalent of the preorbital process. No articulated specimens of *Allocryptaspis* are known, but numerous small plates of *A. laticostata* have been identified with more or less certainty (Denison, 1960, pp. 563–564), and among them is the suborbital (fig. 95,F). In this species the suborbital is a subrectangular plate forming only about one-quarter of the orbital border; as restored (fig. 152,C), the antero-ventral boundary of the orbit is formed by the oral-lateral plate which lies immediately in front of the suborbital. A plate of *Homalaspidella nitida,* tentatively identified by Kiaer and Heintz (1935, pp. 131–132, pl. 30, fig. 1, pl. 33, fig. 1) as a lateral plate, shows some similarities to the presumed suborbital of *Allocryptaspis.*

### Lateral Plates

In pteraspids a variable number of small plates lying between the dorsal shield and the antero-lateral corners of the ventral shield have been called lateral plates (Kiaer, 1928, p. 123; White, 1935, p. 408) or orogonial plates (Stensiö, 1958, p. 258). Probably a single pair of lateral plates is present in *Anglaspis* (fig. 94,A, *lap*). A small lateral plate is found attached to the anterior end of the branchial plate of *Listraspis* (fig. 132, *lap*). A number of lateral plates have been provisionally identified in *Allocryptaspis laticostata* (fig. 95,C, D, E); these have been named antero-lateral, lateral postero-lateral, and medial postero-lateral (Denison, 1960, p. 563). As restored (fig. 152), the postero-laterals abut on one side against notches in the corner of the ventral shield, and on the other side adjoin the suborbital and branchial plates; the antero-lateral is placed ventro-mediad to the suborbital. The plate of *Homalaspidella nitida,* tentatively identified as a lateral plate by Kiaer and Heintz (1935, pp. 131–132), may be a suborbital.

### Oral, Oral-lateral, and Postoral Plates

Oral plates are preserved in the articulated specimens of *Anglaspis heintzi* (fig. 94,A, *orp*), and have recently been described by Heintz (1962, p. 24, fig. 7). This species has relatively few, large oral plates, as compared to the 15 small plates that form the oral cover in the pteraspid, *Protopteraspis vogti* (fig. 94,B). Isolated small, narrow plates of *Allocryptaspis laticostata* (fig. 95,H) have been doubtfully identified as oral plates (Denison, 1960, p. 564).

In pteraspids (White, 1935, pp. 408–412; Heintz, 1962, pp. 19–24) each oral plate has on the inner face of its anterior end a projecting oral tooth lamella (="oral tooth plate" of Kiaer), whose denticulated surface faces the adjacent oral tooth lamella. As shown by Heintz, this indicates that the oral plates did not work against the maxillary brim as believed by Kiaer. The oral plates are imbricated,

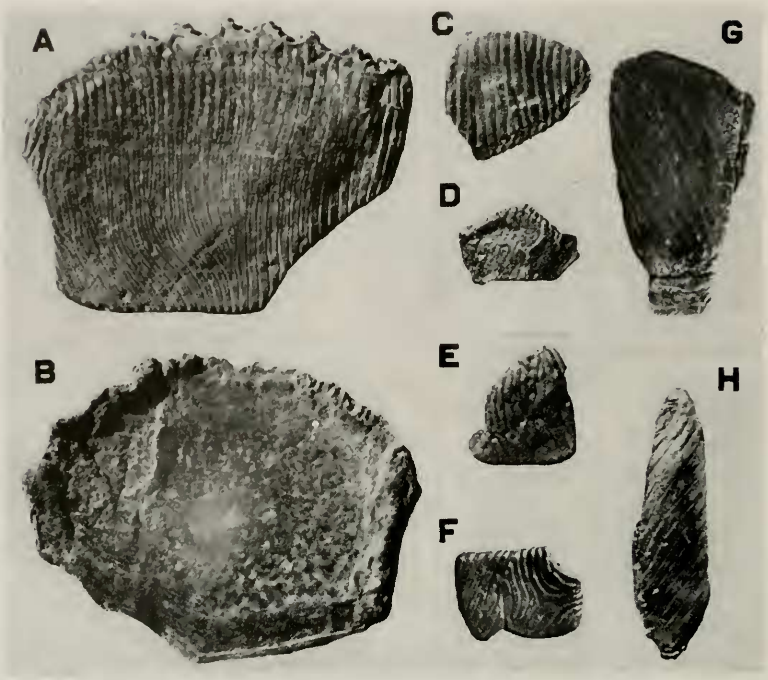

Fig. 95. *Allocryptaspis laticostata;* small plates from anterior part of ventral side of shield (× 4). A, right postoral, PF 1768; B, right postoral, inner side, PF 1763; C, lateral postero-lateral, PF 1782; D, medial postero-lateral, PF 1781; E, antero-lateral, PF 1829; F, suborbital, PF 1777; G, oral-lateral, PF 1780; H, possible oral plate, PF 1776. (From Denison, 1960; specimens in Chicago Natural History Museum.)

which suggests that they were set in infoldings of the skin. This arrangement may have permitted the oral plates to have been protruded, forming a scoop for feeding in bottom sediments. Heintz has suggested the possibility that when the oral plates were protruded, water rich in organic particles may have been drawn into the mouth, and that when the mouth was closed the denticles of the oral tooth lamellae and of the maxillary brim may have served to filter out the food particles. It is also possible that the protruded oral scoop may have had limited ability to pick up selected food particles from the bottom (Denison, 1961, pp. 179–180).

In pteraspids an oral-lateral plate (fig. 94,B, *olp*) lies on either side of the row of oral plates, and is bounded laterally by the rostrum and posteriorly by a lateral plate. No oral-lateral plates are shown in Heintz's figure (1962, fig. 7) of *Anglaspis heintzi.* A plate has been tentatively identified (Denison, 1960, p. 564) as oral-lateral in *Allo-*

*cryptaspis laticostata* (fig. 95,G); as placed in the restoration (fig. 152,C), it extends posteriorly to form a corner of the orbit.

In *Protopteraspis vogti* (fig. 94,B) and *Anglaspis heintzi* (fig. 94,A), there are no postoral plates, and the oral plates articulate directly with the anterior border of the ventral disc. However, postoral plates are well developed in *Allocryptaspis laticostata* (fig. 95,A–B), and were probably arranged much as in *Pteraspis rostrata* (White, 1935, figs. 41–47, 85). The pair of main postoral plates of *Allocryptaspis* attached to the ventral disc posteriorly, to lateral plates at the side, and probably met each other in the midline (fig. 152,C). Between them postero-medially lay two or more small, median postorals, indicated by the shape of the main postorals, and by notches in the anterior margin of the ventral shield.

### Posterior Part of Body and Caudal Fin

Behind the carapace, the posterior body and tail are covered with scales that are best known from Kiaer's reconstruction of *Anglaspis heintzi* (fig. 90), and from Kiaer's and Heintz's (1935, pp. 108–118, figs. 41–50) thorough description of scales of *Poraspis*. In *Allocryptaspis* (Denison, 1953, pp. 302–304, figs. 61, 65,B; 1960, p. 567, fig. 123) the scales are similar to those of *Poraspis*. Anteriorly the scales are relatively very large (fig. 91,C), and are arranged in six longitudinal series: median dorsal, paired dorso-lateral, paired ventro-lateral, and median ventral. The median scales (fig. 96,B–D), dorsal and ventral, are symmetrical, relatively broad and flat anteriorly, and become more and more slender posteriorly. The dorso-lateral scales (fig. 96,A) are extremely large, each usually covering more than half of its side of the ring of scales. The ventro-lateral scales (fig. 96,F) are much smaller, except in *Irregulareaspis hoeli*, where they are nearly equal to the dorso-lateral scales in size (Kiaer, 1932, p. 17, pl. 5). The scales are covered with predominantly longitudinal dentine ridges, though commonly there are one or more anterior ridges at right angles. Each scale, as is usual in fishes, overlaps the scale behind and also the one below. The overlapped margins are anterior brims without dentine ridges, while the posterior or postero-ventral edges that overlap the scales behind have an inner margin with dentine ridges continued from the external surface. In *Pteraspis* the row of ventral ridge scales is broken by a gap that may indicate the position of the anus (White, 1935, p. 418, figs. 65, 85). In *Anglaspis* the anal position may be indicated by a discontinuity posterior to the fourth ventral ridge scale (fig. 90).

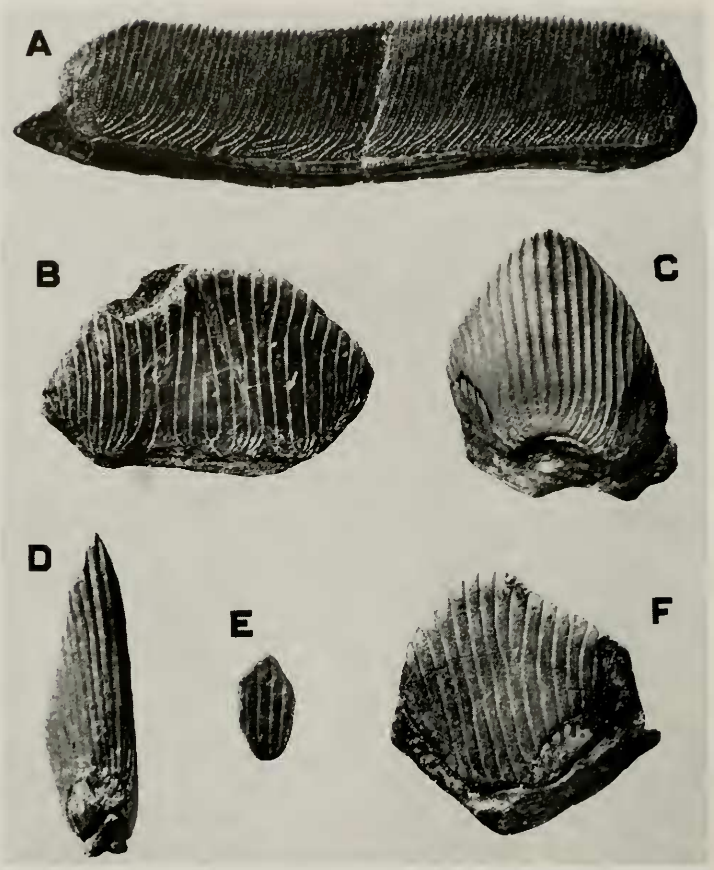

Fig. 96. Scales of *Allocryptaspis laticostata*. A, dorso-lateral scale, PF 1817 (× 3); B, anterior median scale, PF 1814; C, median scale from mid-length, PF 1816; D, posterior median scale, PF 1815; E, caudal scale, PF 1820; F, ventro-lateral scale, PF 1821. (B–F ×9/2.) (From Denison, 1960; specimens in Chicago Natural History Museum.)

On the tail the scales become small and lose the arrangement in longitudinal rows, except that the dorsal and ventral median scales continue as long, slender fulcra (fig. 96,D). The caudal fin itself is somewhat hypocercal in *Anglaspis* with a posteriorly directed lobe projecting ventrally.

Scales are known also in *Tolypelepis* (Pander, 1856, pl. 6, fig. 32), *Cyathaspis*, *Archegonaspis* (Heintz, 1933, figs. 1–2), *Vernonaspis*, *Americaspis*, and *Homalaspidella*. In *Tolypelepis* they are similar to the scale-units that have grown together to form the posterior part of the dorsal shield.

There are never any paired fins in Heterostraci, and their only median one is the caudal fin. There are two reasons for considering this to be a primitive vertebrate condition: (1) paired fins are absent also in primitive Osteostraci, Anaspida, and probably in Coelolepida; (2) it is unlikely from a functional point of view that the heterostracian ancestors would have lost such useful structures had they ever acquired them. On the other hand, Stensiö (1958, pp. 409–413) sees in the cornual plates of pteraspids the vestiges of an ancestral paired fin fold, and in the dorsal and ventral ridge scales the remnants of median fin folds.

The cyathaspids must have been relatively poor swimmers compared to most modern fishes. The carapace made the anterior part of the body inflexible, while the relatively large scales of the posterior part must have resulted in limited flexibility of the only organ of propulsion. In the absence of paired, dorsal, and anal fins, stability in swimming must have been slight, and steering and fine control difficult. However, the large ridge scales, and the dorsal crests and lateral brims of some cyathaspids must have acted as keels to help promote stability.

### Lateral Line Sensory System

In the Cyathaspididae the lateral lines are canals in the cancellous layer of the dermal skeleton (fig. 103,A). These are connected with the surface by small tubes leading to pores, which are usually the only part of the system that is apparent. In some cases, notably in *Poraspis,* the pores are large and prominent, but in a number of genera, for example, *Americaspis,* they are small and difficult to see. On the ventral shield of *Anglaspis insignis* the lateral lines consist of open grooves (fig. 150,B).

The pattern of the canals in this family (fig. 97–99), usually an almost diagrammatically simple combination of longitudinal canals and transverse commissures, has been considered as a primitive arrangement from which could be derived that of other agnathans and gnathostomes. For this reason it has been studied by numerous paleontologists and zoologists, but there is still considerable difference of opinion about the homologies of many canals. Certain identification is possible only if the embryology and innervation are known. This is impossible in Heterostraci, so reliance must be placed on comparison of patterns, and on topographical relationships to the few internal morphological landmarks. Since neither of these procedures is likely to be decisive, the names employed in this paper

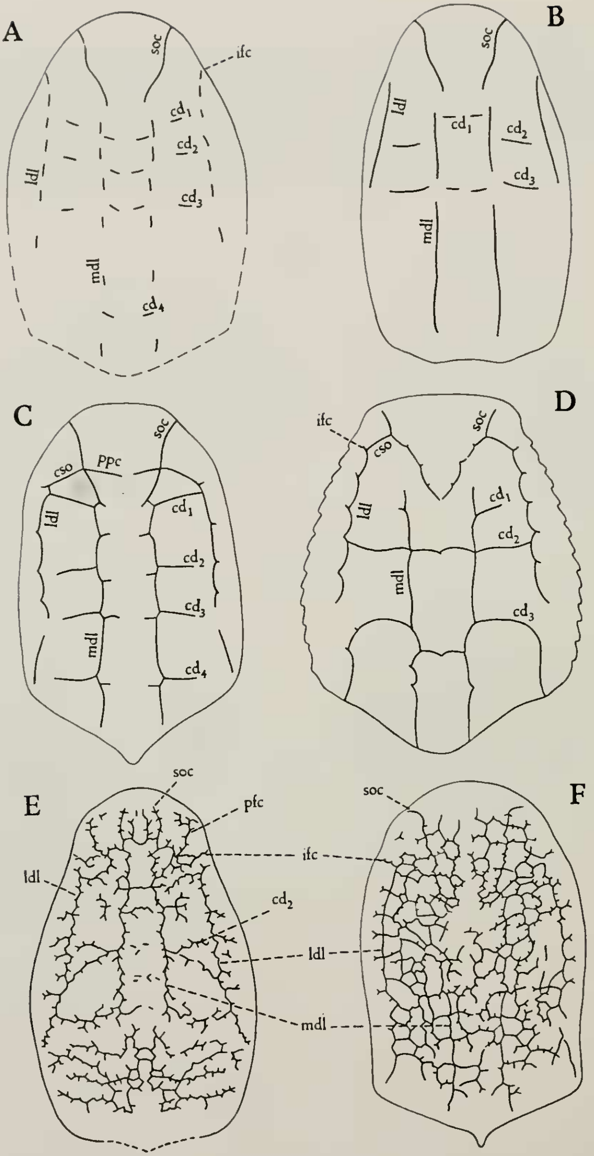

Fig. 97. Dorsal lateral line patterns of Cyathaspidinae, Irregulareaspidinae and Ctenaspidinae. A, *Tolypelepis undulata* (modified after Stensiö, 1958); B, *Ptomaspis canadensis;* C, *Dinaspidella robusta* (from Kiaer, 1932); D, *Ctenaspis dentata* (from Kiaer, 1930); E, *Dikenaspis yukonensis* (pattern restored); F, *Irregulareaspis complicata* (from Kiaer, 1932). For lettering see figure 98.

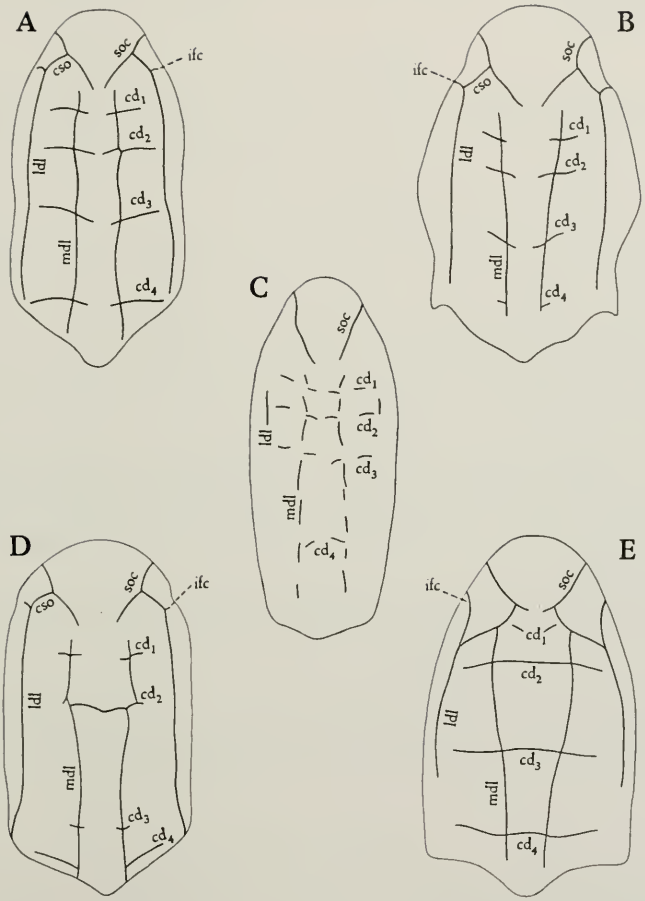

FIG. 98. Dorsal lateral line patterns of Poraspidinae. A, *Poraspis polaris* (from Kiaer, 1932); B, *Anglaspis macculloughi* (mainly after Wills, 1935); C, *Americaspis americana;* D, *Homalaspidella nitida* (from Kiaer, 1932); E, *Allocryptaspis laticostata* (from Denison, 1960).

*$cd_{1-4}$*, first to fourth dorsal transverse commissures; *cso* transverse supraorbital commissure; *ifc*, infraorbital canal; *ldl*, lateral dorsal canal; *mdl*, medial dorsal canal; *pfc*, profundus canal; *ppc*, prepineal transverse commissure; *soc*, supraorbital canal.

are, as far as possible, non-committal, topographical ones; names implying homology are used only when others in common usage are not available.

## DORSAL CANALS

Medial dorsal canals (figs. 97–98, *mdl*), considered by Holmgren (1942, p. 12) to be the main lateral lines of gnathostomes.

Lateral dorsal canals (figs. 97–98, *ldl*), believed by most paleontologists to be the main lateral lines.

Supraorbital canals (figs. 97–98, *soc*), probably homologous, in part at least, to the canals of that name in gnathostomes. The posterior continuations, extending posterior to the pineal organ, have been named the pineal canals by Stensiö (1926, p. 10).

Infraorbital canals (figs. 97–98, *ifc*), probably largely homologous to the infraorbital canals of gnathostomes.

Profundus canals, lying between the orbits and the supraorbital canals. Such canals may occur in *Dikenaspis* (fig. 97,E, *pfc*), Traquairaspididae, and Pteraspididae. They were considered by Holmgren (1942, p. 12) to correspond to the profundus placodes of embryonic *Squalus*.

Transverse supraorbital commissures (figs. 97–98, *cso*), sometimes present to connect the supraorbital and posterior part of the infraorbital canals on either side.

Transverse commissures (figs. 97–98, $cd_{1-4}$), usually four in number in cyathaspids. A prepineal commissure is also present in *Dinaspidella* (fig. 97,C, *ppc*).

## VENTRAL CANALS

Lateral ventral canals (fig. 99, *lvl*), running near the lateral borders of the ventral shield.

Medial ventral canals (fig. 99, *mvl*), continuing the postoral lines posteriorly near the midline in *Homalaspidella* (fig. 99,C) and *Ctenaspis* (fig. 99,F). In other cyathaspids their place is taken by a series of short, obliquely placed canals that are more easily interpreted as transverse commissures (fig. 99, *cvm*) than as segments of longitudinal lines. *Allocryptaspis* (fig. 99,D) has medial longitudinal lines posteriorly, but not anteriorly.

Postoral canals (fig. 99, *pol*), obliquely placed on the anterior part of the ventral shield; these may be considered as the first pair of ventral, transverse commissures.

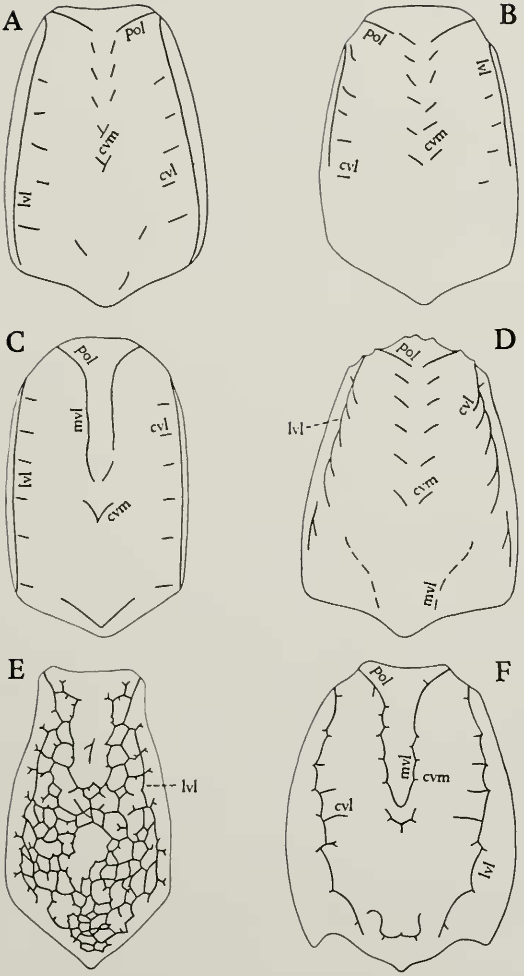

FIG. 99. Ventral lateral line patterns of cyathaspids. A, *Poraspis polaris* (from Kiaer, 1932); B, *Anglaspis insignis* (drawn from photograph published by Kiaer, 1932); C, *Homalaspidella nitida* (from Kiaer, 1932); D, *Allocryptaspis laticostata* (from Denison, 1960); E, *Irregulareaspis hoeli* (from Kiaer, 1932); F, *Ctenaspis dentata* (from Kiaer, 1930).

*cvl, cvm,* lateral and medial ventral transverse commissures; *lvl, mvl,* lateral and medial ventral canals; *pol,* postoral canal.

Ventral transverse commissures, occurring usually as isolated, short, lateral (fig. 99, *cvl*) and medial (fig. 99, *cvm*) canals; six are commonly present in cyathaspids.

The infraorbital canals are the only ones that regularly connect the dorsal and ventral canal systems. There are possibly more posterior connections, however. These are suggested by lateral branches from the lateral dorsal canals of *Dikenaspis* (fig. 97,E), and from the lateral ventral canals of *Allocryptaspis* (fig. 99,D), and also by pores near the anterior ends of the branchial plates of *Poraspis* and *Anglaspis.*

In the dorsal shields of *Tolypelepis* (fig. 97,A) and *Americaspis* (fig. 98,C), the lateral line canals occur as short segments, and it is not unlikely that this is the primitive condition in Heterostraci. An evolutionary trend has been noted in *Poraspis* (Kiaer and Heintz, 1935, p. 126) toward a more regular and complete dorsal pattern, with junctions developing between the posterior ends of the supraorbital (pineal) canals, and between the medial dorsal and supraorbital canals. *Allocryptaspis laticostata* (fig. 98,E) has a relatively complete dorsal pattern. The most striking modification of the lateral line system in cyathaspids is the branching that characterizes the Irregulareaspidinae (fig. 97,E–F). In the extreme case, *Irregulareaspis* (fig. 97,F), the network becomes so complex that it is difficult to recognize individual canals.

Lateral line pores occur commonly on ventro-lateral scales, where they indicate a continuation of one of the ventral longitudinal canals (Kiaer and Heintz, 1935, p. 118, figs. 48, 50, 52). They are relatively rare on either the dorsal or ventral parts of the dorso-lateral scales (op. cit., p. 116, figs. 45h, 47c); these continue one of the dorsal longitudinal canals, and possibly the lateral ventral canal.

## Histology

The microscopic structure of the dermal skeleton of a number of cyathaspids is well known from earlier accounts. *Tolypelepis* has been described by Pander (1856), Rohon (1893), Bystrow (1955), and Gross (1961). An early description of the structure of the shield of *Cyathaspis* was given by Huxley (1858), and of *Americaspis* by Claypole (1885). An excellent description of *Archegonaspis lindstromi* was furnished by Lindström (1895). The histology of *Poraspis* and *Homalaspidella* has been described and figured by Kiaer and Heintz (1935). *Anglaspis* histology has been figured and described by Wills (1935), Bystrow (1955), and Gross (1961). *Sanidaspis* has recently been described by Bystrow (1959). None of these authors has attempted a comprehensive and comparative account of the histology of the different genera of cyathaspids. The microstructure of *Ptomaspis, Seretaspis,* and *Ariaspis* is still completely unknown, and that of *Pionaspis, Listraspis,* and *Dinaspidella* is very inadequately known.

The dermal shield and scales of cyathaspids consist of four layers: (1) the superficial layer, formed by ridges or tubercles of dentine; (2) the reticular layer, immediately under the dentine and consisting of aspidine penetrated by numerous canals; (3) the cancellous layer, formed by aspidine surrounding large chambers; and (4) the basal layer, also of aspidine, forming the inner surface of the shield. The overall thickness of the shield ranges from 0.3 to 1.5 mm. Particularly thin shields occur in *Irregulareaspis* (0.3 mm.) (fig. 101,B), *Homalaspidella* (0.3 mm.) and *Dikenaspis* (.35 –.40 mm.) (fig. 101,A), and especially thick shields are found in *Sanidaspis, Allocryptaspis* (fig. 102,C), and some *Poraspis,* in which they are often over 0.9 mm. The thickness may be considerably reduced by crushing, typically of the relatively weak cancellous layer.

The *superficial layer* is present in all cyathaspids except *Ctenaspis,* and consists of ridges, and sometimes of tubercles, of dentine, separated by intercostal grooves. The dentine and a thin layer of aspidine around the intercostal grooves are the first parts of the dermal skeleton to form, as is shown by thin sections of juvenile *Cyathaspis* cf. *acadica* (fig. 159,A) and *Allocryptaspis laticostata* (fig. 159,B). In the former, the dentine is only 15–30$\mu$ thick, while in the latter it is about 35$\mu$. In later stages of the formation of the shield, additional laminae of dentine are added on the inner side of the ridge so that the dentine commonly becomes 50–80$\mu$ thick, and may be as much as 120–130$\mu$ in fully adult *Archegonaspis, Poraspis,* and *Anglaspis.* In younger individuals with thin dentine, the central pulp canal is wide and continuous (fig. 159); in fully adult ridges or tubercles with thicker dentine, the pulp canal is usually narrow, and is sometimes (*Anglaspis, Tolypelepis*) divided into chambers connected by canals (fig. 103,B). *Allocryptaspis* (fig. 102,C, 104,A) and *Sanidaspis,* in which the dentine ridges are unusually wide, have two longitudinal pulp canals in each dentine ridge. From a pulp canal dentine tubules extend toward the surface of a ridge. Usually they pass more or less directly toward the surface, that is at right angles to the direction of the ridge and pulp canal, but in those forms with a chambered

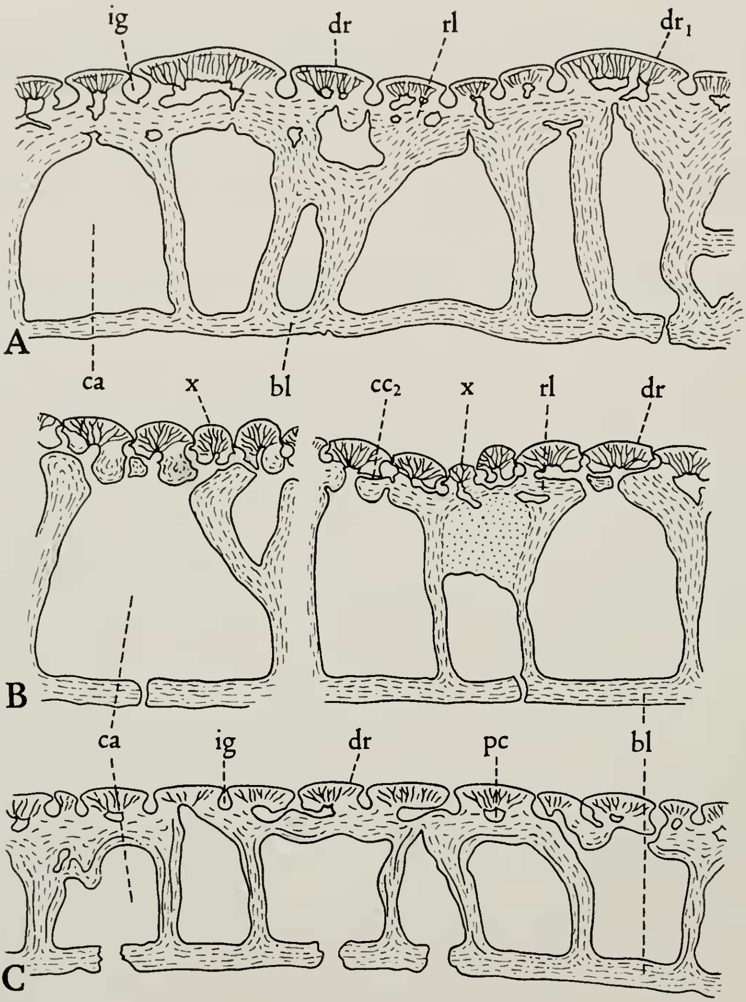

FIG. 100. Transverse sections through dermal shields of Cyathaspidinae (× 50). A, *Cyathaspis banksi*, CNHM, slide 4027; B, *Archegonaspis lindstromi*, after Lindström, 1895; C, *Vernonaspis sekwiae*, CNHM, slide 4029. For lettering see figure 101.

pulp canal (*Anglaspis, Tolypelepis,* and perhaps *Poraspis sericea*) they tend to radiate from each chamber. This was taken by Bystrow (1959, p. 62) to be evidence that the dentine ridges were formed phylogenetically by the coalescence of denticles. In *Allocryptaspis laticostata* (fig. 104,A) the dentine tubules occur in small clusters, each cluster arising from a small pocket projecting from the pulp

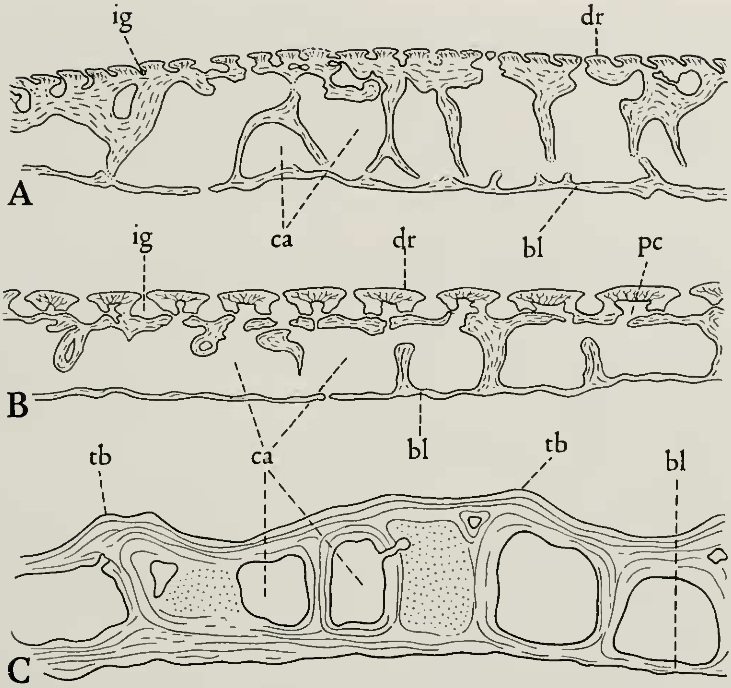

FIG. 101. Transverse sections through dermal shields of Irregulareaspidinae and Ctenaspidinae (× 50). A, *Dikenaspis yukonensis*, CNHM, slide 4037; B, *Irregulareaspis* sp., CNHM, slide 4591; C, *Ctenaspis dentata*, CNHM, slide 4049.

*bl*, basal layer; *ca*, chamber of cancellous layer; $cc_2$, canal connecting pulp canal to intercostal groove; *dr*, dentine ridge; $dr_1$, large, elevated dentine ridge; *ig*, intercostal groove; *pc*, pulp canal; *rl*, reticular layer; *tb*, tubercle; *x*, line of meeting of central and lateral epitega.

canal. The tubules are generally somewhat irregular, and branch one or more times between the pulp canal and their termination near the surface. The surface of a ridge sometimes has a thin, transparent, enamel-like layer that may be vitrodentine rather than true enamel.

Transverse sections of various genera and species of cyathaspids (figs. 100–102) may often be distinguished by differences in the width and shape of the dentine ridges. Ridges are very narrow in *Dikenaspis* (fig. 101,A) and *Listraspis* (0.06–0.08 mm.), and narrow in *Irregulareaspis* (fig. 101,B) and *Pionaspis* (0.12–0.14 mm.). They are especially broad in *Sanidaspis, Allocryptaspis* (fig. 102,C) and *Anglaspis* (fig. 102,D) (0.25–0.45 mm.). The crest of a ridge may be flat, gently rounded, strongly convex, or sharply angular; this character has been used commonly in the systematic revision to distinguish genera and species. In *Tolypelepis* and *Cyathaspis* (fig. 100,A) the presence of wider and higher ridges separated by a few narrower and lower ridges is distinctive. The margins of a ridge, where the surface turns down into the intercostal grooves, is generally rounded or sharp-edged; in *Archegonaspis lindstromi* (fig. 100,B) one side of a ridge usually has a double edge and the other side a single edge. The ridge margins commonly appear to be straight, but in a number of genera they are gently scalloped; these are *Tolypelepis* (Pander, 1856, pl. 6, fig. 24*c*), *Cyathaspis* (CNHM, PF 1493), *Archegonaspis* (Lindström, 1895, pl. 2, figs. 5–6), *Poraspis* (Kiaer and Heintz, 1935, fig. 18), *Anglaspis* (Gross, 1961, figs. 6–7), and *Allocryptaspis* (fig. 104,B). In these forms the adjacent dentine ridges may be in contact at the projections of the scalloped edge so that the intercostal grooves open only by narrow slits between the contacts.

The *intercostal grooves* (Kiaer and Heintz, 1935, p. 74;= mucous grooves of Stensiö, 1932, and White, 1935; or Zwischenrinne of Gross, 1961) separate the dentine ridges and tubercles. In an early stage of the formation of the shield or scales (fig. 159), thin laminae of aspidine surround these grooves and are continuous with the dentine laminae of adjacent ridges. These two tissues were undoubtedly formed simultaneously and, as pointed out by Gross (1961, p. 145), differ only in the presence or absence of dentine tubules. The intercostal grooves are usually 30–50 μ in diameter, though they may be as much as 60–70 μ in *Anglaspis* and *Allocryptaspis*. Their base usually lies 60–70 μ below the crests of the dentine ridges, but is as much as 160 μ in *Anglaspis* because of the high-crested ridges. The grooves in cross-section are commonly more or less round, but they are pear-shaped in *Dikenaspis* and tear-drop-shaped in *Poraspis* (fig. 102,A). In some cyathaspids the intercostal grooves open continuously to the surface by a narrow slit between adjacent dentine ridges. In sections of *Irregulareaspis* sp. (fig. 101,B), this slit is about 20–30 μ wide, but usually it is much narrower. As pointed out above, in a number of cyathaspids the intercostal grooves open

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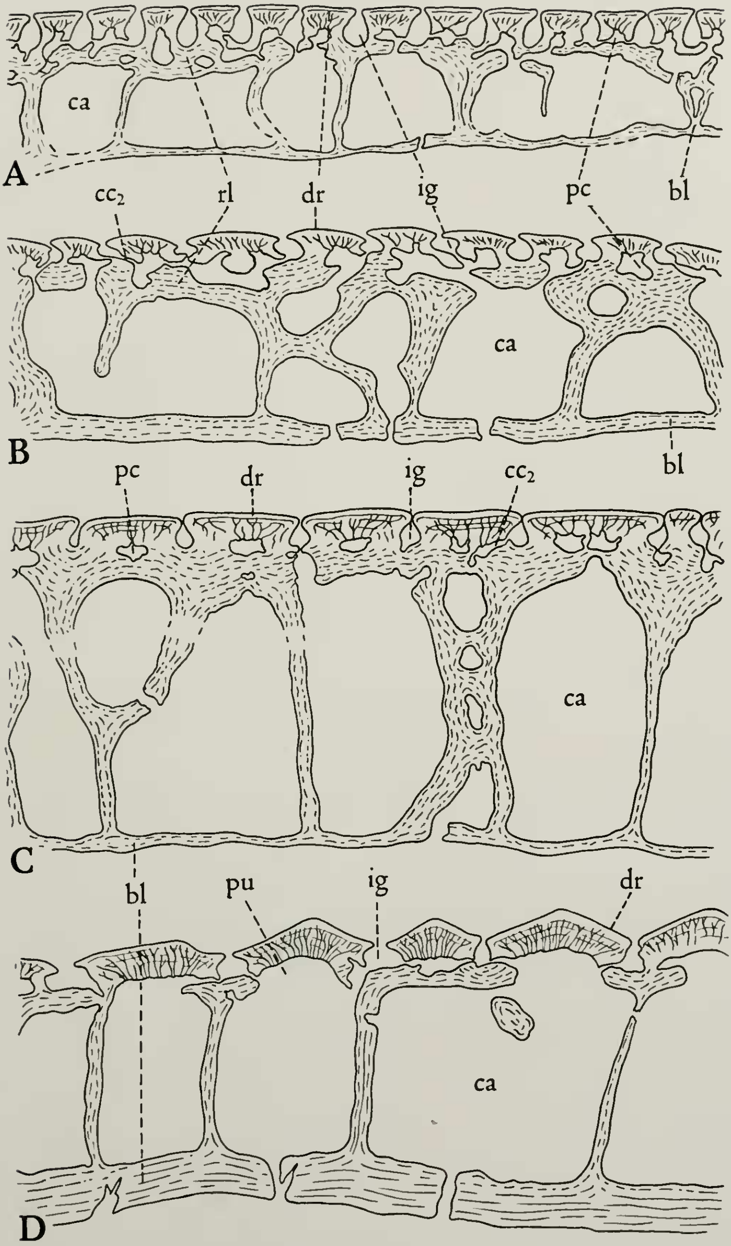
FIG. 102. Transverse sections through dermal shield of Poraspidinae (× 50). A, *Poraspis polaris*, CNHM, slide 4038; B, *Americaspis* sp., CNHM, slide 4588; C, *Allocryptaspis laticostata*, CNHM, slide 4045; D, *Anglaspis macculloughi*, CNHM, slide 4041.

*bl*, basal layer; *ca*, chamber of cancellous layer; *cc*$_2$, canal connecting pulp canal to intercostal groove; *dr*, dentine ridge; *ig*, intercostal groove; *pc*, pulp canal; *pu*, pulp chamber; *rl*, reticular layer.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only by rows of slit-like pores between the partially contiguous scalloped edges of adjacent dentine ridges.

The intercostal grooves are probably homologous to the pore-canal system of Osteostraci, Crossopterygii, and Dipnoi. In these groups, the system consists of mesh-canals (Maschenkanäle) that form a network typically just below the surface of the dermal bones, and of pore-canals (Porenkanäle) that connect the mesh-canals with the surface (Gross, 1956). The intercostal grooves resemble this system in their superficial position, in their cross-section, and in their vascular supply (Gross, 1961, p. 145). In Osteostraci, Crossopterygii, and Dipnoi, the pore-canal system is related to the lateral lines, and for this reason is believed to be a sensory system, probably sensitive to currents acting on the body (Denison, 1947, pp. 350–353; Bölau, 1951, pp. 38–39; Gross, 1956, p. 136; Dijkgraaf, 1963, pp. 78–81). The lateral lines of cyathaspids lie in the cancellous layer, well below the intercostal grooves. However, White (1935, p. 421, fig. 66a) has shown in pteraspids that the lateral lines communicate with the intercostal grooves, and a thin section of *Irregulareaspis* sp. (fig. 103,A) shows a lateral-line canal passing into two adjacent intercostal grooves. The intercostal canals may have been filled with mucous, but the production of mucous was not their chief function (Gross, 1956, p. 96).

The *recticular layer* is a relatively thin part of the dermal skeleton lying below the dentine ridges and superficial to the chambers of the cancellous layer. It is composed of aspidine, but the manner of its formation is not certain. According to Gross (1961, p. 145), the vessels passing through this layer are surrounded by fine lamellae that form skeletal tubes comparable to primary osteons. I have been unable to confirm this, except in the case of the intercostal grooves, which are surrounded by aspidine lamellae continuous with the dentine lamellae. On the other hand, an obliquely tangential section of *Allocryptaspis laticostata* (fig. 104,C) shows this layer to be composed of cross-fibered aspidine continuous with that of the cancellous layer; there is no clear indication of any lamellation around the canals, and the arrangement of the fibers does not appear to be governed by the canals. In *Ctenaspis dentata* (fig. 101,C), where the superficial layer is absent, aspidine of the reticular layer forms the surface and is clearly lamellate parallel to the surface, rising in the tubercular elevations and sinking in the depressions between. In skeletons of juvenile individuals the reticular layer may be mostly or completely absent, a condition that at times has been used mistakenly as a systematic character. In the absence of this layer, the pulp canals open widely and directly into the chambers of the cancellous layer.

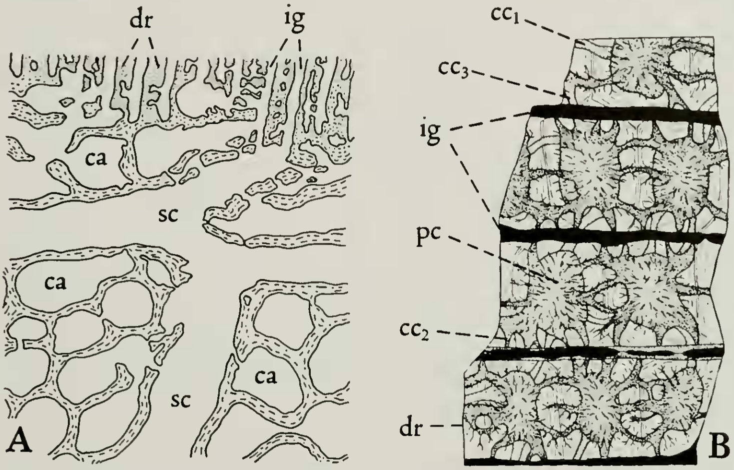

FIG. 103. A, oblique section through superficial, reticular and cancellous layers of dermal shield of *Irregulareaspis* sp., CNHM, slide 4590 (× 25); B, tangential section through superficial layer of *Anglaspis* sp. (from Gross, 1961) (× 50). *ca*, chamber of cancellous layer; *cc*$_1$, longitudinal canal connecting pulp chambers; *cc*$_2$, canal connecting pulp chamber to intercostal groove; *cc*$_3$, canal connectting pulp chambers of adjacent dentine ridges; *dr*, dentine ridge; *ig*, intercostal groove; *pc*, pulp chamber; *sc*, lateral line sensory canal.

The outstanding feature of the reticular layer is its numerous canals which bring vascular and nervous supply to the superficial structures. These canals are: (1) Pulp canals of the dentine ridges (figs. 100–103, *pc*); when these canals are paired, as in *Allocryptaspis* (fig. 104,A) and *Sanidaspis,* there are numerous cross connections between the members of a pair; or where the pulp canals are divided into chambers, as in *Tolypelepis* and *Anglaspis,* there are longitudinal canals (fig. 103,B, *cc*$_1$) connecting the chambers. (2) Canals lateral from pulp canals to the intercostal grooves; these are abundant and regular in *Poraspis* (fig. 102,A), *Americaspis* (fig. 102,B, *cc*$_2$), and *Sanidaspis;* they emerge from each of the pulp chambers of *Anglaspis* (fig. 103,B, *cc*$_2$); they are relatively few in number in *Allocryptaspis* (fig. 102,C, *cc*$_2$). (3) Canals passing laterally from the pulp canals and continuing under the intercostal grooves; in *Anglaspis* (fig. 103,B, *cc*$_3$) they may connect directly with the pulp canal of the neighboring ridge; in *Allocryptaspis* they meet vertical or oblique canals leading from the cancellous layer to intercostal grooves.

(4) Vertical canals from the cancellous layer to pulp canals. (5) Vertical or oblique canals from the cancellous layer to intercostal grooves; these are very numerous in *Allocryptaspis laticostata* (fig. 102,C). A thin section of *Ctenaspis dentata* (fig. 101,C) is remarkable for the scarcity of canals in the reticular layer.

The *cancellous layer* is the weakest part of the dermal skeleton, and is often crushed. In *Allocryptaspis laticostata,* for example, only in pyritized specimens is it preserved uncrushed. This layer consists of large chambers (fig. 100–104, *ca*), commonly polygonal in tangential section, separated by more or less vertical septae, floored by the basal layer, and covered by the recticular layer. In those specimens that have a well-developed reticular layer, the cancellous layer usually occupies 55–72 per cent of the total thickness of the central part of a shield. *Allocryptaspis laticostata* (fig. 102,C) has an unusually deep cancellous layer, which may occupy 78 per cent of the thickness of the shield. Near the margins of a shield, the chambers may become very small. The width of the chambers is usually 200–400 $\mu$, but Bystrow (1959, fig. 2) shows them 800 $\mu$ wide in *Sanidaspis,* and some are at least 670 $\mu$ wide in *Allocryptaspis.* The chambers are surrounded by lamellar aspidine. This is clearly shown in sections of *Ctenaspis dentata* (fig. 101,C) and of *Irregulareaspis* sp. (CNHM, slides 4589–90), also in figures of *Anglaspis* sp. (Gross, 1961, fig. 6, C, D). A thin section of *Allocryptaspis laticostata* (CNHM, slide 4594) shows a cross-fibered structure continuous with that of the reticular layer, but the lamination is only faintly suggested by color differences. In younger cyathaspids there are relatively few laminae, and the septae between the chambers are thin. The septae become thicker with age by the formation of additional laminae. They have been found most commonly to be 30–70 $\mu$ thick, but in *Allocryptaspis laticostata* they have been measured as thin as 20 $\mu$ and as thick as 130 $\mu$. The chambers are irregular in shape, size, and arrangement in *Dikenaspis* (fig. 101,A) and *Irregulareaspis* (figs. 101,B, 103,A). In *Poraspis* they are usually regular and hexagonal in section, except near the margin of the shield. In *Anglaspis* (fig. 102,D) they are regularly arranged in rows under the dentine ridges, one chamber corresponding in width to one ridge, and with the septae underlying the intercostal grooves. In *Allocryptaspis laticostata* (figs. 102,C, 104,C–D) they are also arranged under the dentine ridges, but the regularity is less than in *Anglaspis,* and the correspondence of ridges and chambers is not perfect. In most cyathaspids more than one dentine ridge overlies a chamber,

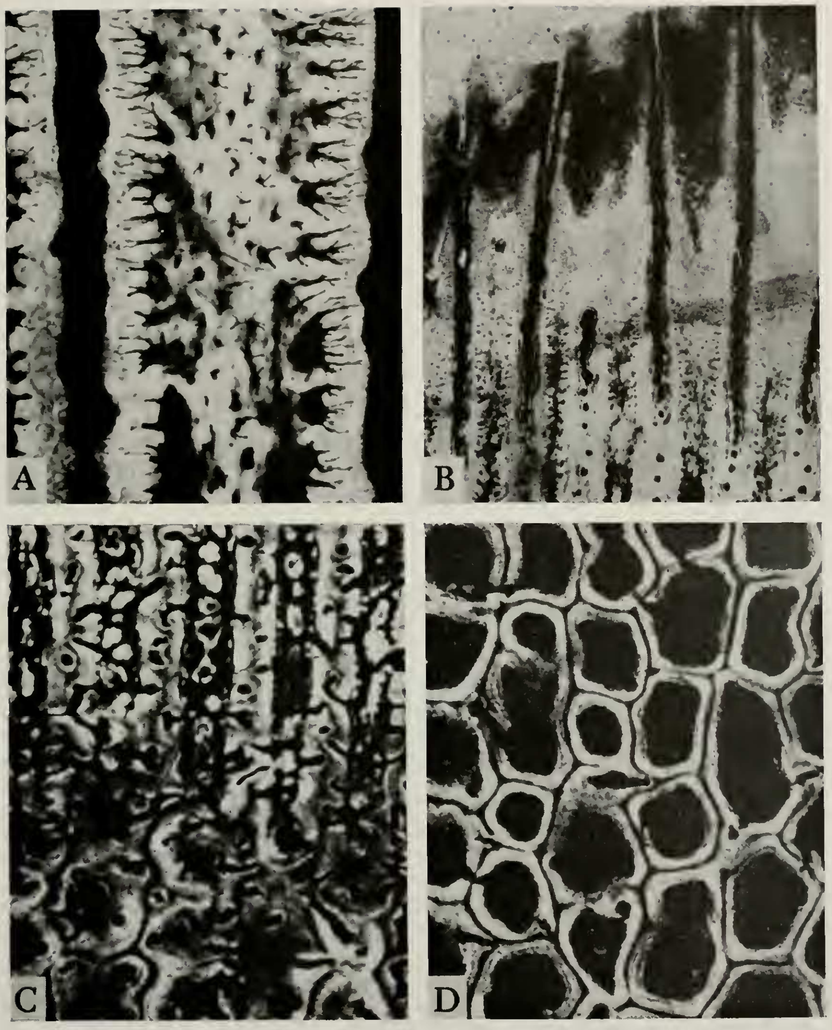

FIG. 104. Tangential or obliquely tangential sections through dermal shield of *Allocryptaspis laticostata*. A, Dentine ridge and two intercostal grooves, showing clusters of dentine tubules arising from pulp chambers; CNHM, slide 4594 (× 90). B, Oblique section through superficial layer (at top) and reticular layer, showing parts of five dentine ridges and six intercostal grooves, the latter with small slit-like openings at the surface; CNHM, slide 4597 (× 30). C, An oblique section through the reticular layer; CNHM, slide 4594 (× 30). D, A tangential section through the cancellous layer; CNHM, slide 4596 (× 30).

and a linear arrangement of chambers is lacking. There are commonly perforations in the septae giving communication between adjacent chambers. There are numerous pores in the roof of the chambers, leading into the many canals of the reticular layer. Lateral line canals, 150–360 μ in diameter, lie in the upper half of the cancellous layer; their external connections are with pores and intercostal grooves by means of branch canals (fig. 103,A, *sc*).

The *basal layer* consists of lamellae of aspidine, some of which are part of the layers concentric around overlying chambers (fig. 101,C). In well-preserved material Sharpey's fibers may be seen penetrating it (Gross, 1961, fig. 6). The basal layer is thin or absent in newly forming shields, and thickens with age by the addition of laminae. Bystrow (1955, fig. 11) shows it very thin in an incompletely developed *Tolypelepis,* and very thick in sections of *Poraspis sericea* (200 μ, op. cit., fig. 17) and *Sanidaspis* (120 μ, Bystrow, 1959, fig. 2). Vertical canals pass through the basal layer to supply the cancellous and overlying layers.

*Comparisons.*—In the microstructure of the dermal shield, the Pteraspididae are very close to the Cyathaspididae. Both families are characterized by the possession of a cancellous layer with large chambers separated by more or less vertical septae. This is in striking contrast to most other Heterostraci (Psammosteidae, *Astraspis, Eriptychius, Cardipeltis, Weigeltaspis,* and *Tesseraspis*) in which the middle layer is a more typical spongiosa with smaller cavities separated by irregular partitions. In *Corvaspis* large chambers of the cyathaspid type occur at the center of plates, and a spongy bone at the margins (Dineley, 1953, fig. 16). In *Traquairaspis* (Wills, 1935, pl. 6) large chambers occur under the smooth area of the central disc, while the middle layer of the rest of the shield is spongy. The initial stage in the development of the pteraspid shield is similar to that of cyathaspids. Thin sections of ventral discs of juvenile *Protaspis* sp. (CNHM, slides 4069–70) about 12 mm. long show only a thin capping of dentine on the ridges and a thin trabecula of aspidine surrounding each intercostal groove. Later stages of pteraspid growth have not yet been studied in detail histologically; however, in addition to growth of individual plates around their periphery, the plates apparently grow in thickness by the addition of laminae of aspidine to the inner surface of the basal layer. This leads eventually to the development of a thicker basal layer than is typically found in cyathaspids.

## Internal Structure

No member of the Heterostraci has yet been found with any mineralized internal skeleton, and it is not likely that such was ever developed in this order. For this reason there can be little direct information about the internal anatomy of the group. There are a few external indications of the position of internal structures: the mouth, orbits, pineal macula, and external branchial openings. In addition, a number of cyathaspids and a few pteraspids, especially the smaller ones, preserve impressions of internal organs on the inner side of the dermal shield (figs. 106, 132, 151,A, 156). Those structures that are quite certainly interpretable are parts of the brain, pineal organ, vertical semicircular canals, and gills. Some years ago Stensiö (1932, fig. 65) produced a reconstruction of the internal anatomy of cyathaspids, and recently (1958) he has attempted a different and more elaborate one. Since there is such limited factual basis for a reconstruction, Stensiö's are only understandable as attempts to adapt the structure of a myxinoid to a heterostracian shield. Some points of his later reconstruction will be considered critically in the following discussion of the cyathaspid internal anatomy.

*Mouth and Nostrils:* The ventral border of the rostrum of cyathaspids forms a maxillary brim (subrostral lamina of Stensiö) that is variously ornamented with ridges and denticles of dentine (fig. 105, *mxb*). This is generally believed to be the dorsal (or anterior) border of the mouth. The ventral (or posterior) border of the mouth is formed by a series of oral plates (fig. 94) which lie opposite to the maxillary brim in a few articulated specimens of pteraspids (*Protopteraspis vogti,* Kiaer, 1928, pl. 12; Heintz, 1962, figs. 1–6; *Pteraspis rostrata,* White, 1935, figs. 41–47) and cyathaspids (*Anglaspis heintzi,* Heintz, 1962, fig. 7). In his latest attempt to adapt the Heterostraci to the myxinoid plan, Stensiö (1958, pp. 342–350) has found it necessary to insert between the oral plates and maxillary brim a palatosubnasal lamella, which separates a prenasal sinus from the buccal cavity. There is absolutely no evidence for this structure, and it is clearly impossible to fit it in such an articulated, relatively uncrushed specimen as the figured examples of *Protopteraspis vogti* (fig. 105).

It is generally believed that the nasal sacs were situated in paired depressions on the inner side of the dorsal shield just posterior to the maxillary brim (Heintz, 1962, p. 25). The presence or absence of external nares has not been clearly demonstrated. Kiaer and Heintz (1935, p. 69, pl. 26, fig. 1) showed in the ventral border of a preorbital process of a specimen of *Poraspis polaris* a notch which they interpreted as a nasal opening. Watson (1954, p. 12) described but did not figure rounded notches at the lateral ends of the maxillary brim of *Anglaspis macculloughi;* these he interpreted as nostrils, and compared their position to that of lungfishes. Stensiö (1958, fig. 193) showed similarly placed notches in *Poraspis pompeckji*, but he interpreted them as probably housing tentacles. Nostrils in the position of these notches would be bounded medially by oral-lateral or possibly lateral plates. Openings in this position are not apparent in any articulated pteraspids or cyathaspids, and so their existence is doubtful. If external nostrils were absent, the olfactory organs presumably opened into the anterior part of the buccal cavity. In Stensiö's latest reconstruction (1958, figs. 190, 200), the nasal capsules are unpaired, lie just in front of the pineal organ, and are connected with the exterior by the hypothetical naso-hypophysial duct and prenasal sinus.

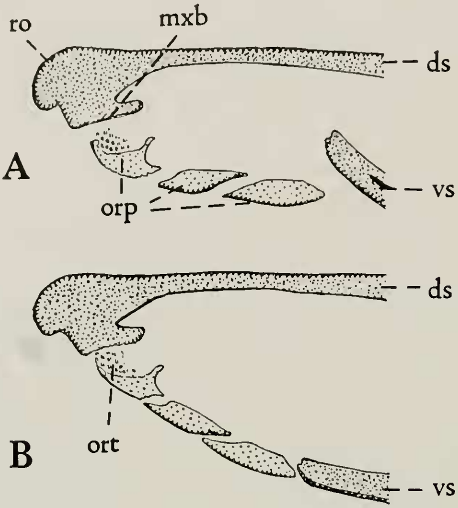

Fig. 105. Sagittal sections through anterior part of shield of *Protopteraspis vogti* (from Heintz, 1962). A, as preserved; B, as restored.

*ds*, dorsal shield; *mxb*, maxillary brim; *orp*, oral plates; *ort*, oral tooth lamella; *ro*, rostrum; *vs*, ventral shield.

*Brain.*—The pineal organ, usually indicated by the pineal macula externally (fig. 91,A, *pm*), and by a corresponding pit on the inner side of the dorsal shield (figs. 106, 132,A, 151,A, 155, 156, *pfo*), is the most important landmark in the anterior part of the brain. It is logical to assume that it lay, as in lampreys, at the anterior end of the diencephalon, and that the telencephalon lay antero-ventrally to it. There is no evidence that the forebrain was crowded as in embryonic myxinoids, as claimed by Stensiö (1958, p. 374). The position of the myelencephalon is indicated on the inner side of the shield by a relatively broad groove that tapers posteriorly into the groove for the spinal cord (figs. 106, 132,A, 155, *br*).

*Semicircular canals.*—The pair of V-shaped markings on either side of the myelencephalon indicate the position of the anterior and posterior vertical semicircular canals (figs. 106, 132,A, 151,A, 155, 156, *scc*). It has generally been assumed that the horizontal semicircular canals were absent as in cyclostomes; however, because of their deeper position they could not have left any mark on the dermal shield, so it is perfectly possible that they were present in Heterostraci.

*Gills and Visceral Arches.*—The series of paired impressions on either side of the dorsal and ventral shields has been recognized since Woodward's identification (1891, p. xvii) as indicating gill chambers (fig. 91, $k_2$–$k_8$). Between the gills we may safely assume the presence of a visceral skeleton, possibly of cartilage. The points requiring discussion are the homology, number, type, and functioning of the gills and their arches.

Säve-Söderbergh (1941, p. 531) made the assumption that the first postorbital visceral arch, that is, the one lying immediately anterior to the first gill pouch, was the segment innervated by the trigeminal nerve. Stensiö (1958, p. 378) agreed with this interpretation. Watson's (1954, p. 15) identification of gill pouches in *Anglaspis* is confusing because apparently he identified as the first pair some markings between the orbits labeled "*de*" by Wills (1935, p. 433, fig. 2B). I have been unable to find these markings on Chicago Natural History Museum specimens of *Anglaspis macculoughi*. There is a marking here only on one side of the figured specimen of *A. insignis* (Kiaer, 1932, pl. 6, fig. 1). These markings are definitely absent on *A. expatriata* (fig. 151,A), *Poraspis* (fig. 106), *Seretaspis*, "*Archegonaspis*" *drummondi* (fig. 156), and *Pteraspis*, so it is unlikely that "*de*" represents gill pouches. Watson's "third" pouch is lateral to the ampulla of the anterior vertical semicircular canal, the "second" pouch he identifies as "hyoidean or spiracular," and so the visceral arch anterior to it would be the mandibular arch; it is the one so identified by Säve-Söderbergh and Stensiö.

Homology of individual gills with those of gnathostomes can best be determined by innervation, and in Heterostraci that can only be suggested by topographical relations to other cranial landmarks. Of the latter, the best is the vestibular region as marked by the semicircular canals. Typically in vertebrates, the facial nerve issues anterior to the vestibular region, and the glossopharyngeal nerve posterior to it. Assuming that these nerves sent their post-trematic branches nearly directly laterad to the adjacent gill arch (which is not necessarily so), either the second or the third visceral arch of cyathaspids is hyoidean. I know no evidence which permits a more precise determination. The second arch is the one identified by Säve-Söderbergh, Watson, and Stensiö as hyoidean. If, on the other hand, the third is hyoidean, then both mandibular and premandibular arches would be present in Heterostraci.

The number of gills in Heterostraci can be determined only by the number of impressions on the dorsal and ventral shields. Since these are sometimes incompletely preserved, and commonly not indicated at all, it is difficult to generalize about the total number. Stensiö (1958, pp. 384, 387–388) considered the number of gills as a character of taxonomic importance, and claimed that there are 5 to 11 innervated by the vagus, meaning 8 to 14 in all. It will be necessary to consider in detail the evidence for Stensiö's counts. Before doing this, it should be pointed out that Stensiö labels the first pouch "$k_2$," so that the total number is one less than the labelled number of the most posterior gill. Stensiö presents the following figures as evidence:

*Poraspis pompeckji*, fig. 179A, a photograph. $k_2$–$k_9$ are labeled, but $k_8$ is the most posterior one visible, and the most posterior one shown in his drawing, fig. 193, and in another photograph, fig. 206.

*Poraspis cylindrica*, fig. 179B, a photograph. $k_2$–$k_9$ are labeled, but $k_9$ does not show on his photograph, nor on a cast of this specimen (my fig. 106).

*Homalaspidella nitida*, fig. 180B, a photograph. $k_2$–$k_8$ are labeled, but only $k_2$–$k_7$ appear on the photograph (see also Kiaer and Heintz, 1935, pl. 30, fig. 3).

*Anglaspis insignis*, fig. 180A, a photograph, and fig. 205B, a drawing. $k_2$–$k_9$ are labeled, and $k_{10}$–$k_{11}$ are added in the drawing, but $k_8$ is the most posterior shown on the photograph and on a cast of this specimen.

*Anglaspis macculloughi*, fig. 205A, a drawing. $k_2$–$k_{12}$ are shown. Watson (1954, p. 10) says there are 10–11 gills in this species, but Wills (1935, p. 433, fig. 2B) indicates that it has only seven ($k_2$–$k_8$).

*Seretaspis zychi*, fig. 204, a photograph. $k_2$–$k_9$ are labeled, but the photograph and the specimen show only $k_2$–$k_8$.

*Archegonaspis integra*, fig. 202, a drawing. Shows $k_2$–$k_9$.

*Protopteraspis primaeva*, fig. 197B, a drawing. Shows $k_2$–$k_9$, but photographs, figs. 197A and 199A, show only $k_2$–$k_8$.

FIG. 106. *Poraspis cylindrica;* dorsal shield preserved largely as an internal impression and showing molds of gill pouches, pineal fossa, semicircular canals and cranial cavity (from Kiaer, 1932). Type, Paleontologisk Museum, Oslo, D 205 (× about 2).

It will be noted that no evidence is presented for more than seven pairs of gills (that is, $k_2$–$k_8$). Precisely the same seven pairs are present in "*Archegonaspis*" *drummondi* (fig. 156), *Listraspis canadensis* (fig. 132,A), *Vernonaspis sekwiae*, *V. vaningeni*, and *Anglaspis expatriata* (fig. 151,A). Only six can be seen in *Allocryptaspis elliptica* (Bryant, 1935, fig. 1, and pl. 5), and in *Homalaspidella nitida* (see p. 344). The seventh gill ($k_8$ of Stensiö) lies just in advance of of the external branchial opening, and it is probable that there were no gills behind it, and no posterior branchial ducts or other related structures inferred by Stensiö (1958, pp. 393–394).

The impressions of the gills on the dorsal and ventral shields indicate that the gill chambers were transversely arranged, very high dorso-ventrally, and short antero-posteriorly (Watson, 1954, pp. 10–11, figs. 4, B, C). A series of corresponding small impressions lateral to the main gill impressions (fig. 91,A, $lk_{2-8}$) have been interpreted as representing extrabranchial atria by Stensiö (1958, pp. 389–391), but Watson (loc. cit.) believed that they were formed by the exhalant ducts of each gill. The atria or ducts probably opened on either side into a common branchial duct, sometimes marked by a groove on the inner side of the branchial plate, and perhaps on the adjacent part of the lateral epitegum. The common branchial duct opened to the exterior at the external branchial opening, which lies close behind the most posterior gill chamber. Watson believed that the gills were pouches of adult cyclostome pattern, but there are important differences. In cyclostomes the gills are relatively small, rounded pouches, surrounded by muscles and by peribranchial sinuses. In cyathaspids the gills occupied a large percentage of the volume within the shield, and because of their impressions on the dermal shield, could not have been covered by either muscles or sinuses. Stensiö (1958, pp. 375, 399) believed that the gills were not pouch-like, but were more of the type inferred in Osteostraci. He interpreted a series of grooves crossing the gill markings of *Poraspis, Seretaspis,* and *Protopteraspis* as imprints of gill lamellae (op. cit., p. 366, figs. 199A, 203A, 204). This interpretation is questionable, since it is hard to imagine how gill lamellae could have left markings on the dermal skeleton. It is possible that these grooves are indications of a visceral endoskeleton, or of blood vessels. In conclusion, it appears that too little is known about heterostracian gills to compare them in any detail with those of other groups.

Watson (1954, pp. 10–12) and Stensiö (1958, pp. 395–397) have both considered the manner in which cyathaspid gills might have functioned. They pointed out that the carapace was effectively of fixed volume, and that this made impossible inspiration and expiration by means of movements of the whole pharyngeal region. Ciliary currents were considered to be inadequate, and muscles that could contract the gills were presumably absent. Therefore, they inferred the presence of a muscular pump to induce the respiratory current, and have considered that it may have been a velum such as pumps water to the gills of *Myxine*.

The visceral endoskeleton may have been formed of cartilage, or perhaps merely of stiffened connective tissue. It is not necessarily the coherent structure with extensive connections to the endocranium that Stensiö reconstructs (1958, fig. 198). If, as I have suggested above, there were no gills posterior to the branchial opening, then the visceral skeleton did not extend as far posteriorly as shown by Stensiö. He shows a clearly marked posterior limit for the visceral endoskeleton in *Poraspis cylindrica* (1958, fig. 179B, *l. visc. p*); this marking is not present in the original figure of this specimen (Kiaer, 1932, pl. 3, fig. 3), or in a Chicago Natural History Museum cast of it (fig. 106). Stensiö also shows the posterior limit of the visceral endoskeleton in a drawing of *Anglaspis macculloughi* (1958, fig. 205A), but this does not appear in Wills' (1935) figures, or in Chicago specimens of this species. It is clearly absent in the type of *Anglaspis expatriata* (fig. 151,A) in the position shown by Stensiö.

## RELATIONSHIP OF HETEROSTRACI

Since the Heterostraci, to which the Cyathaspididae belong, are the earliest known vertebrates, their relationship to other vertebrate groups is of considerable significance. There has been, and still is, a divergence of opinion regarding their systematic position. The history of that opinion has been reviewed by Kiaer (1924, pp. 113–119) and Kiaer and Heintz (1935, pp. 19–31), so only the most significant contributions need be mentioned here. In 1889, Cope referred both the living cyclostomes ("Marsipobranchii") and fossil "Ostracodermi" (including Heterostraci) to the Class Agnatha. In 1932 Kiaer subdivided the Agnatha into two different groups: (1) the Monorhina, including the Osteostraci, Anaspida, and Cyclostomata, all characterized by an unpaired nasal opening, and (2) the Diplorhina, including the Heterostraci and Coelolepida, with paired nasal openings. A somewhat different form of this classification had previously been offered in 1924 by Kiaer. In 1927 and 1932 Stensiö proposed another grouping: the Osteostraci, Anaspida, and Petromyzonida were grouped in one subclass (Cephalaspidomorphi), while the Heterostraci and Myxinoidea were grouped in another subclass (Pteraspidomorphi). This classification has been defended in his recent (1958) interpretation of heterostracian structure. Today there is broad agreement, at least among paleontologists, that the Osteostraci, Anaspida, and Petromyzonida are related, but there is lack of agreement about the relationship of the Heterostraci, and about the possibility of a biphyletic origin of Cyclostomata. Some points bearing on these questions will be discussed here.

One of the most striking morphological features of the Petromyzonida is the presence of an unpaired naso-hypophysial opening on the dorsal side of the head. This unusual arrangement results from the great enlargement during development of a post-hypophysial fold or "upper lip," which comes to form the rostral part of the head. The naso-hypophysial opening is dorsally placed in Osteostraci and Anaspida, and so it is probable that these groups also had a similar development of the anterior head region. In the Myxinoidea the arrangement is somewhat different. The post-hypophysial fold enlarges, but not as much, and the single nostril finally becomes terminal rather than dorsal in position. The naso-hypophysial duct acquires an opening into the pharynx, and the post-hypophysial fold forms a "secondary palate" separating this duct from the buccal cavity. It is probable, but not yet demonstrated, that the myxinoid condition had a common ancestry with the forerunners of Petromyzonida in which there was enlargement of the post-hypophysial fold. There is no evidence that Heterostraci partook of these features at all. The nostrils were probably paired and opened into the anterior buccal cavity, and the nasal sacs are believed to have been dorsal to them. This being so, there was no enlargement of the post-hypophysial fold, and the rostral region was fundamentally different from that of Cyclostomata, Osteostraci, and Anaspida, and similar to that of gnathostomes.

The Petromyzonida have only two pairs of semicircular canals, and Myxinoidea have only one, though the latter may each represent the two canals of Petromyzonida. Only two pairs of vertical canals leave impressions in Heterostraci, but this can hardly be taken as evidence of the absence of the horizontal canals; as pointed out above (p. 343), the latter are too deep to leave impressions on the dermal skeleton. The gills of Heterostraci have been compared to those of cyclostomes, but they surely had little resemblance to the gill pouches of adult lampreys and hagfishes. Actually there is little evidence about the type of gills present in Heterostraci, though their size and extent are indicated. The single pair of external branchial openings is a point of resemblance to *Myxine*, but not to other cyclostomes. The long list of characters cited by Stensiö (1958, pp. 414–415) in which the Heterostraci are supposed to resemble cyclostomes in general, and myxinoids in particular, are largely characters of his reconstruction, and not of Heterostraci at all. I would therefore agree with Kiaer (1924, 1932), White (1935), Obruchev (1945), Wängsjö (1952), Watson (1954), Balabai (1956), Tarlo (1962a), and Heintz (1962) that there is no close relationship of

Heterostraci to Cyclostomata, Osteostraci, and Anaspida. These groups can be classified as follows:

- Class Agnatha
  - Subclass Diplorhina (=Pteraspidomorphi)
    - Order Heterostraci
    - ?Order Coelolepida
  - Subclass Monorhina
    - Superorder Hyperotreti
      - Order Myxinoidea
    - Superorder Hyperoartii
      - Order Petromyzonida
      - Order Osteostraci
      - Order Anaspida

The Monorhina are unquestionably more specialized than the Diplorhina in the structure of the anterior head region. The Diplorhina have their specializations also, but in a number of important features the Cyathaspididae are extremely primitive vertebrates. The gill chambers and the presumed intervening arches form a very uniform series, not crowded posteriorly by the formation of jaws as in gnathostomes, and unmodified by the development of a huge oralo-branchial chamber as in Osteostraci, or of a rasping tongue as in lampreys. It is possible that a relatively unmodified premandibular arch is present. The lateral line system is often quite completely developed, and has a simple pattern from which that of other agnathans and gnathostomes could be derived. The presence of a dermal skeleton and the absence of a calcified endoskeleton may be primitive (Denison, 1964, p. 150). The absence of paired fins, and probably of dorsal and anal fins, is surely primitive (for a contrary opinion, see Stensiö, 1958, pp. 409–413). It is regrettable that there is no preservable endoskeleton in Heterostraci from which more of the structure of these primitive vertebrates could be determined.

## SYSTEMATIC REVISION

This work is intended primarily as a taxonomic revision of North American Cyathaspididae. Although new diagnoses are presented for all genera, I have restricted myself in most cases to no more than nomenclatorial revision of European species. The family Cyathaspididae, as used here, is equivalent to the suborder Cyathaspida of Kiaer (1932), and the subfamilies of this paper are approximately equivalent to the families of Kiaer. The characteristics used to distinguish the various categories are mostly derived from the dorsal shield.

*Subfamilies* are distinguished largely by: (1) presence or absence of apparent scale components in the shield; (2) presence or absence of distinct epitega; (3) the pattern, length and uniformity of the superficial dentine ridges. Certain subfamilies are distinguished in part by the proportions and shape of the shield, the fineness of the dentine ridges, the branching of the lateral lines, and the absence of the superficial layer.

*Genera* are distinguished by: (1) distinctness of epitega, postrostral field, and pineal macula; (2) pattern, length, shape, coarseness, and uniformity of dentine ridges; (3) shape of the shield, the presence or absence of a median rostral process, and the development of the preorbital processes and postbranchial lobes; (4) proportions, (particularly the width), orbital, pineal, and postbranchial ratios; (5) pattern, subdivision, reduction, and branching of the lateral line canals. Other characters used in certain genera are: presence of lateral brims or laminae, and of median crests and spines on the dorsal shield; development and ornament of maxillary brim; presence or absence of postoral plates; ornament when superficial layer is absent; histology; and size, if unusually large or small.

*Species* are distinguished primarily by: (1) size, usually measured by the median length of the dorsal shield; (2) coarseness of dentine ridges, as measured by the number of ridges per millimeter, preferably on the central part of the dorsal shield; and (3) proportions, especially the width, orbital and pineal ratios. In addition, in some cases I have also used the rostral ridge pattern, the shape of the dentine ridge crests, and the shape of the rostral and posterior edges of the dorsal shield.

## CYATHASPIDIDAE

This family includes small Heterostraci whose carapace consists of a dorsal shield, a ventral shield, paired branchial, oral, lateral, and suborbital plates. There may be postbranchial lobes but no cornual plates. A dorsal spine is typically absent. The rostrum is not extended, and the ventrally-placed mouth is subterminal. The orbits are bounded above by the dorsal shield and below by suborbital plates. The branchial openings typically lie between the dorsal shield and the branchial plates. There are probably only seven pairs of gills. Scales are of relatively large size, and include median dorsal, dorso-lateral, ventro-lateral, and median ventral rows. Except in *Ctenaspis*, the external surface is ornamented with dentine ridges that have smooth or gently scalloped edges. The chambers of the cancellous layer are usually large and separated by more or less vertical septae. The lateral lines are canals in the cancellous layer that open to the surface by pores; they are arranged in a simple pattern consisting of two pairs of longitudinal canals dorsally and ventrally, transverse commissures, infraorbital, and supraorbital, and perhaps profundus lines.

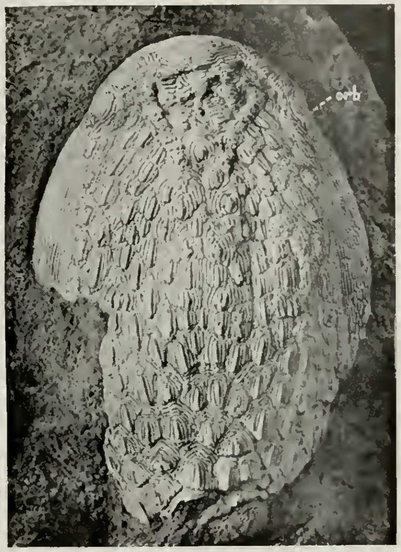

FIG. 107. *Tolypelepis undulata*, dorsal shield (× 2). (From Kiaer, 1932.)
*orb*, orbit.

## Tolypelepidinae

The dorsal shield appears to be composed in part of fused scales, and is divided into distinct epitega. Most dentine ridges are short, and the central ridges of the scale components are broader and higher than the surrounding ridges. The central ridge pattern is elliptical, the rostral pattern is transverse, and a postrostral field may be distinguished. *Tolypelepis.*

### **Tolypelepis** Pander

*Type-species.—Tolypelepis undulatus* Pander.

*Tolypelepis* Pander, 1856, Mon. foss. Fische Sil. Syst. russ.-balt. Gouvern., pp. 60–61; Lindström, 1895, Bihang K. Svensk. Vetensk.-Akad. Handl., **21**, Afd. 4, Nr. 3, p. 10; Strand, 1934, Folia Zool. Hydrobiol., **5**, pp. 327–328; Flower and Wayland-Smith, 1952, Bull. Mus. Comp. Zool., **107**, p. 370; Denison, 1953, Fieldiana: Geol., **11**, no. 7 p. 293; Bystrow, 1955, Akad. Nauk. SSSR, Mem. Vol. A. S. Berg, pp. 481–486; Stensiö, 1958, Traité de Zool., **13**, fasc. 1, pp. 297–307; Gross, 1961, Acta Zool., **42**, p.145.

*Tolypaspis* F. Schmidt, 1893, Neues Jahrb. Min. Geol. Pal., **1893**, vol. 1, p. 100; Rohon, 1893, Mém. Acad. Imp. Sci. St. Petersbourg, (7), **41**, no. 5, pp. 76–79, 119–120; Zych, 1931, Fauna Ryb Dewonu i Downtonu Podola, p. 83; Kiaer, 1932, Skr. Svalbard Ishavet, **52**, p. 25.

*Tolpyaspis* (in error) Rohon, 1893, Mém. Acad. Imp. Sci. St. Petersbourg (7), **41**, p. 76.

*Oniscolepis* (in part) Pander, 1856, Mon. foss Fische Sil. Syst russ.-balt. Gouvern., pp. 56–58.

*Tolepelepis* (in error) Tarlo, 1960, Palaeontology, **3**, p. 223.

*Diagnosis.*—The shield is broad and the preorbital length is rather short (orbital ratio=.14). On the central epitegum and postrostral field the dentine ridges are short and are grouped into scale-like areas, with narrower, lower ridges arranged around a coarser, higher central ridge.

### **Tolypelepis undulata** Pander. Figures 97,A, 107.

*Tolypelepis undulatus* Pander, 1856, Mon. foss. Fische Sil. Syst. russ.-balt. Gouvern., p. 61, pl. 6, figs. 24a–d.

*Tolypelepis undulata* Denison, 1953, Fieldiana: Geol., **11**, no. 7, p. 292; Bystrow, 1955, Akad. Nauk. SSSR, Mem. Vol. A. S. Berg, pp. 481–485, figs. 10–12; Stensiö, 1958, Traité de Zool., **13**, fasc. 1, figs. 169A–B, 170, 215; Gross, 1961, Acta Zool., **42**, pp. 108–109, figs. 12M–N.

*Tolypaspis undulata* F. Schmidt, 1893, Neues Jahrb. Min. Geol. Pal., **1893**, vol. 1, p. 100; Rohon, 1893, Mém. Acad. Imp. Sci. St. Petersbourg, (7), **41**, no. 5, pp. 79–88, fig. 17, pl. 1, fig. 45, pl. 2, figs. 54, 56; Hoppe, 1931, Palaeontogr., **76**, Abt. A, p. 58; Kiaer, 1932, Skr. Svalbard Ishavet, **52**, p. 25, pl. 10; Gross, 1950, Abh. Deutsch. Akad. Wiss. Berlin, Math.-Nat. Kl., **1949**, Nr. 1, p. 51.

*Tolypaspis schmidti* (in error) Zych, 1931, Fauna Ryb Dewonu i Downtonu Podola, p. 83.

*Oniscolepis magnus* Pander, 1856, Mon. foss Fische Sil. Syst. russ.-balt. Gouvern. pp. 56, 58, pl. 6, fig. 32*a–c*.

*Oniscolepis magna* Rohon, 1893, Mém. Acad. Imp. Sci. St. Petersbourg (7), **41**, pp. 79, 81–82, 89; Gross, 1947, Palaeontogr., **96**, Abt. A, p. 96; 1961, Acta Zool., **42**, p. 108.

*Type.*—Shield fragment figured by Pander (1856, pl. 6, fig. 24).

*Occurrence.*—Late Silurian, Upper Oesel Group ($K_4$), Ohesaare-Pank, Oesel.

*Diagnosis.*—The length of the dorsal shield is 33 to 36 mm. and its width ratio is .67. The dentine ridges have rounded crests and average about 4 per mm., but the largest are about 2 per mm., and the smallest on the lateral epitega are about 8 per mm.

*Discussion.*—Because Pander's original description of *Tolypelepis undulata* was based on a small shield fragment, Schmidt (1893) introduced the new name *Tolypaspis* in describing a nearly complete shield of the same species. One species of *Oniscolepis, O. magna* Pander, has been referred to *Tolypelepis* by Rohon (1893, pp. 81–82) and by Gross (1947, p. 96; 1961, p. 108). However, Pander's other species of *Oniscolepis, O. crenulata, O. dentata,* and *O. serrata,* are not cyathaspids, and may be related to *Strosipherus* (Gross, 1961, pp. 100–101).

The reference to this species by Rohon (1893, p. 79) of specimens from the Ludlow Bone Bed of England is doubtful; his reference (loc. cit.) to "*Tolypaspis*" of specimens from the "cornstones" of Ledbury, England is probably incorrect.

### Tolypelepis cf. undulata

*Tolypelepis* cf. *undulata* Gross, 1961, Acta Zool., **42**, pp. 76, 108.

*Occurrence.*—Late Silurian, glacial erratics of Beyrichienkalk, North Germany.

### Tolypelepis timanica Kossovoy and Obruchev

*Tolypelepis* cf. *undulata* Sokolov, 1962, 2nd Internat. Arbeitstagung über die Silur/Devon-Grenze und die Stratigraphie von Silur und Devon, Bonn-Bruxelles, 1960, Symposiums-Band, p. 252.

*Tolypelepis timanica* Kossovoy and Obruchev, 1962, Doklady Akad. Nauk SSSR, **147**, p. 1149 (nomen nudum).

*Occurrence.*—Early Devonian, probably Late Downtonian, Eptarmenskaya beds, Velikaya River, northern Timan (approximately 67° 21′ N., 48° 33′ E.), USSR.

*Discussion.*—This species has only been listed.

### Tolypelepis sp.

*Tolypelepis* sp. White, 1946, Quart. Jour. Geol. Soc. London, **101**, p. 212.

*Occurrence.*—Late Downtonian (zone of *Traquairaspis pococki*), Herefordshire, England.

*Tolypelepis* n. sp. A Thorsteinsson, 1958, Geol. Surv. Canada, Mem. **294**, p. 47.

*Occurrence.*—Middle Silurian (Early Wenlockian, zone of *Monograptus riccartonensis*), near top of Allen Bay formation on Shellabear Creek, and member C of Cape Phillips formation on north coast, Cornwallis Island, Canada.

### Cyathaspidinae

Epitega are distinct, but there is little or no trace of scale components on the shield. Most of the dentine ridges are long. The ridge pattern is slightly elliptical or nearly longitudinal on the central epitegum, and transverse, in part at least, on the rostral epitegum; the postrostral field may be distinct. *Ptomaspis, Cyathaspis, Archegonaspis, Seretaspis, Vernonaspis, Pionaspis, Listraspis.*

### **Ptomaspis** Denison

*Type-species.—Ptomaspis canadensis* Denison.

*Ptomaspis* Denison, 1963, Fieldiana: Geol., **14**, no. 7, pp. 113–114, 140.

*Diagnosis.*—The dorsal shield is of moderate proportions; its orbital notches are anteriorly placed and shallow, and its posterior margin is gently convex. The dentine ridges include some that are slightly higher between others that are lower and sometimes slightly narrower; they are subdivided into short lengths or even into small denticles. Locally, but especially on the posterior part of the dorsal shield, the ridges are grouped into scale-like areas with parallel ridges. The rostral epitegum has short transverse ridges anteriorly, and grades through a denticulate area into antero-posterior ridges in the postrostral field.

### **Ptomaspis canadensis** Denison. Figures 97,B, 108, 109.

*Ptomaspis canadensis* Denison, 1963, Fieldiana: Geol., **14**, no. 7, p. 116, figs. 64–65.

*Type.*—Princeton 17090, a nearly complete dorsal shield (figs. 108, 109).

*Occurrence.*—Probably Early Devonian (Early Downtonian) limestones and graptolitic shales,[1] Beaver River, southeastern Yukon.

*Diagnosis.*—The length of the dorsal shield is 61 mm. The width ratio is .58. Dentine ridges average about 5 per mm.

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[1] Tentatively assigned to the Middle Ludlovian in Denison (1963); see below (pp. 450–451).

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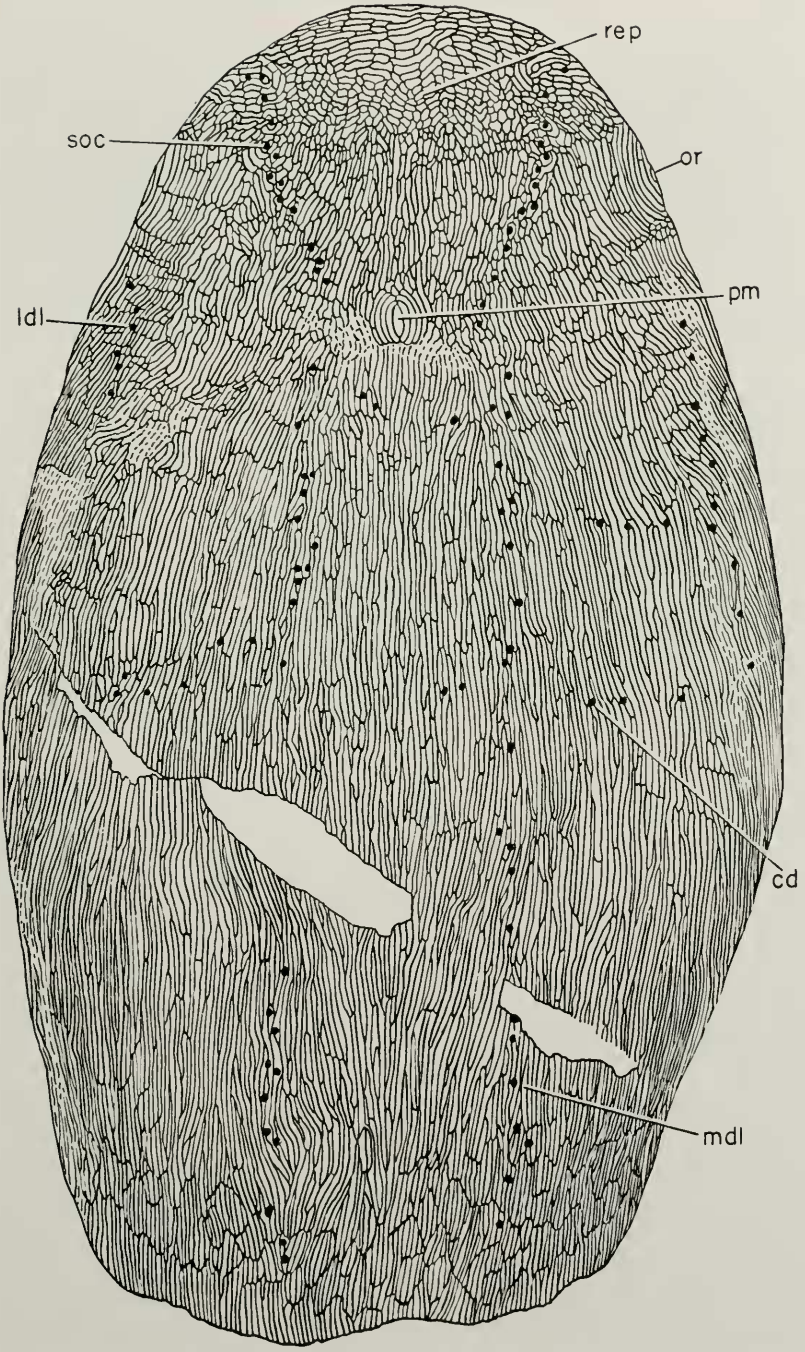
FIG. 108. *Ptomaspis canadensis*, type; dorsal shield, Princeton 17090 (× 3). (From Denison, 1963.)

*cd*, pores of dorsal transverse sensory commissure; *ldl*, *mdl*, pores of lateral and medial dorsal sensory canals; *or*, orbit; *pm*, pineal macula; *rep*, rostral epitegum; *soc*, pores of supraorbital sensory canal.


rep
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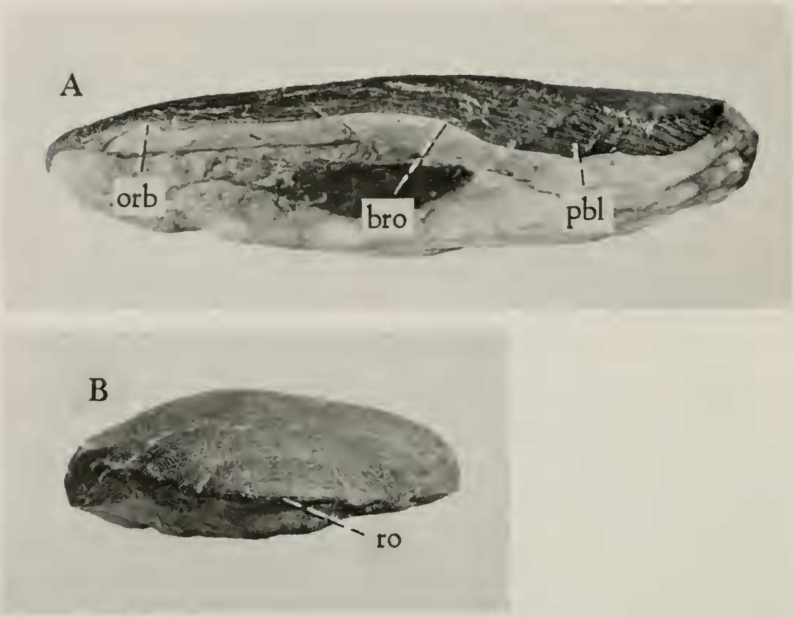

Fig. 109. *Ptomaspis canadensis*, type; dorsal shield, Princeton 17090 (× 3/2). A, ventro-lateral view; B, rostral view.

*bro*, branchial opening; *orb*, orbit; *pbl*, postbranchial lobe; *ro*, rostrum.

*Discussion.*—The outstanding characteristic of *Ptomaspis* is the retention of scale-like areas of ornamentation on the dorsal shield. This primitive feature relates it to *Tolypelepis,* but in the latter the scale-like areas are more distinct and extend over the whole central epitegum and onto the postrostral field (fig. 107), while in *Ptomaspis* they are clearly marked only on the posterior part of the dorsal shield (fig. 108). In the presence of higher and sometimes broader ridges surrounded by lower and narrower ridges, *Ptomaspis* resembles a number of other Cyathaspididae—*Cyathaspis, Tolypelepis,* and some *Archegonaspis.* This is also believed to be a primitive characteristic, but is well along on the road to reduction and loss in *Ptomaspis.* The pattern of the lateral line system (fig. 97,B) is indicated by distinct pores and appears to be typical of the family; the lateral and medial dorsal lines are probably nearly continuous instead of being broken into short lengths as in *Tolypelepis.* *Ptomaspis* resembles *Archegonaspis* in lacking a median rostral process (fig. 109,B) and in having long but slightly developed postbranchial lobes (fig. 109,A, *pbl*). It is intermediate between the Tolypelepidinae and Cyathaspidinae.

### **Cyathaspis** Lankester

*Type-species.—Pteraspis banksii* Huxley and Salter.

*Pteraspis* (in part) Huxley and Salter, 1856, Quart. Jour. Geol. Soc. London, **12**, p. 100.

*Cyathaspis* Lankester, 1865, Rept. Brit. Assoc. Adv. Sci., **1864**, Not. and Abstr., p. 58; 1868, Fishes Old Red Sandstone, Mon. Pal. Soc., p. 26; Von Alth, 1886, Beitr. Pal. Geol. Österr.-Ung., **5**, Heft 3, pp. 63–69, 72, 73; Woodward, 1891, Cat. Fossil Fishes Brit. Mus. (Nat. Hist.), **2**, p. 170; Claypole, 1892, Quart. Jour. Geol. Soc. London, **48**, pp. 543–546; Lindström, 1895, Bihang K. Svensk. Vetensk.-Akad. Handl., **21**, Afd. 4, no. 3, p. 9; Leriche, 1906, Mém. Soc. Géol. Nord, **5**, pp. 22–25; Zych, 1931, Fauna Ryb Dewonu i Downtonu Podola, p. 84; Kiaer, 1932, Skr. Svalbard Ishavet, **52**, pp. 21–22; Kiaer and Heintz, 1935, Skr. Svalbard Ishavet, **40**, p. 32; Heintz, 1938, Naturwissensch., **28**, p. 51, fig. 2*c;* Flower and Wayland-Smith, 1952, Bull. Mus. Comp. Zool., **107**, p. 365; Denison, 1953, Fieldiana: Geol., **11**, no. 7, pp. 292–293; Stensiö, 1958, Traité de Zool., **13**, fasc. 1, pp. 307–310, 312, 314–316, 319.

*Scaphaspis* (in part) Lankester, 1865, Rept. Brit. Assoc. Adv. Sci., **1864**, Not. and Abstr., p. 58.

*Diplaspis* Matthew, 1887, Bull. Nat. Hist. Soc. New Brunswick, no. **6**, pp. 69–73; Kiaer, 1932, Skr. Svalbard Ishavet, **52**, p. 25; Flower and Wayland-Smith, 1952, Bull. Mus. Comp. Zool., **107**, p. 371; Denison, 1953, Fieldiana: Geol., **11**, no. 7, p. 293; Stensiö, 1958, Traité de Zool., **13**, fasc. 1, pp. 312–314.

*Diagnosis.*—The dorsal shield is broad and truncate posteriorly. The central epitegum is strongly arched, and the lateral epitega form broad, flat brims. There is a postero-median crest on both the dorsal and ventral shields. The orbits are situated anteriorly (orbital ratio=.11–.14), but the pineal organ is rather posterior (pineal ratio=.24–.28). On the central epitegum and central part of the ventral shield there are a few coarse dentine ridges separated by 1 to 5 finer ridges; elsewhere the ridges are of uniform size. The ridges have a rounded convex crest. The ridge pattern is elliptical on the central epitegum and central part of the ventral shield. There is usually a band of ridges parallel to the anterior and lateral edges of the ventral shield.

*Discussion.*—In addition to its shape, one of the most distinctive characters of the *Cyathaspis* shield is the presence on the central areas of coarser ridges separated by one or a few finer ridges (fig. 100,A, $dr$, $dr_1$). Among the Cyathaspididae this feature is most strongly developed in *Tolypelepis* where each scale-like area has a coarse central ridge. It is shown to a slight extent in *Ptomaspis* and *Archegonaspis integra.* Stensiö (1958, p. 310) states that it is present also

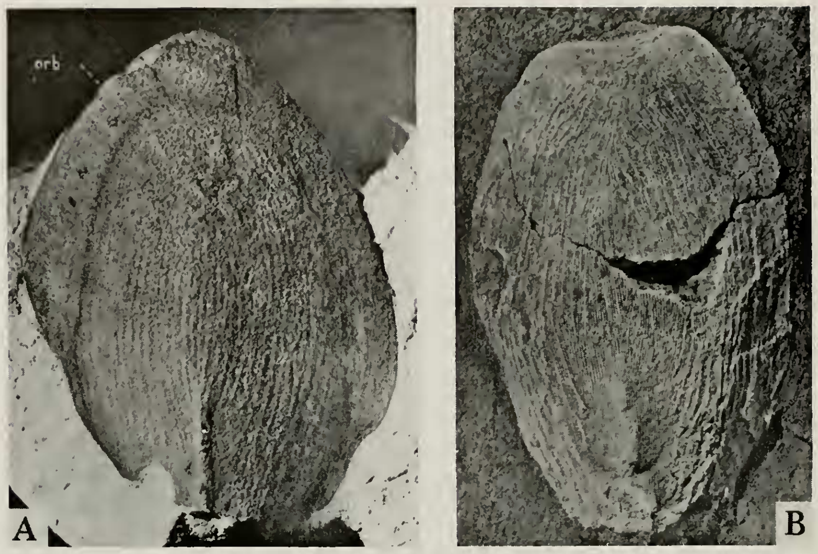

FIG. 110. *Cyathaspis banksi* (from Kiaer, 1932); specimens in collection of Geological Survey of Great Britain (× about 3). A, dorsal shield; B, ventral shield.

*orb*, orbit.

in *Archegonaspis ludensis* but this is apparently in error; the specimen to which he refers (Brit. Mus. P. 3241) is *Cyathaspis banksi.*

Kiaer (1932, p. 22) stated that *Cyathaspis* had a "real dorsal spine" comparable to that of *Pteraspis,* but judging from his own figure (op. cit., pl. 8, fig. 2), and according to Lankester (1868, p. 26), this is not a distinct element, but only a crest on the central epitegum.

**Cyathaspis banksi** (Huxley and Salter). Figures 100,A, 110.

*Pteraspis banksii* Huxley and Salter, 1856, Quart. Jour. Geol. Soc. London, **12**, p. 100, pl. 2, fig. 2*a–d;* Huxley, 1858, Quart. Jour. Geol. Soc. London, **14**, pp. 274–277, pl. 15; von Alth, 1886, Beitr. Pal. Geol. Österr.-Ung., **5**, Heft 3, p. 64.

*Pteraspis truncatus* Huxley and Salter, 1856, Quart. Jour. Geol. Soc. London, **12**, p. 100, pl. 2, fig. 1*a–d;* Salter, 1859, Ann, Mag. Nat. Hist., (3), **4**, pp. 45–47, fig. 2.

*Cyathaspis banksii* Lankester, 1865, Rept. Brit. Assoc. Adv. Sci., **1864**, Not. and Abstr., p. 58; 1868, Fishes Old Red Sandstone, Mon. Pal. Soc., pp. 26–27, pl. 2, figs. 9–11, pl. 4, fig. 6.

*Scaphaspis truncatus* Lankester, 1865, Rept. Brit. Assoc. Adv. Sci., **1864**, Not. and Abstr., p. 58; 1868, Fishes Old Red Sandstone, Mon. Pal. Soc., pp. 24–25, pl. 2, figs. 1–3.

*Cyathaspis banksi* Woodward, 1891, Cat. Fossil Fishes Brit. Mus. (Nat. Hist.), **2**, pp. 171–172, pl. 9, fig. 3; Leriche, 1906, Mém. Soc. Géol. Nord, **5**, pp. 23–24, fig. 5; Jaekel, 1927, Zeits. Ges. Anat., 3 Abt., Ergebn. Anat. Entwickl., **27**, p. 877, fig. 25; Kiaer, 1932, Skr. Svalbard Ishavet, **52**, p. 22, pl. 8; White, 1950, Bull. Brit. Mus. (Nat. Hist.), Geol., **1**, p. 54; 1958, Studies on Fossil Vertebrates, ed. Westoll, p. 218; Stensiö, 1958, Traité de Zool., **13**, fasc. 1, fig. 171.

*Type.*—Dorsal shield, not designated.

*Occurrence.*—Late Silurian (Late Ludlovian, Upper Whitcliffe Beds) and Early Devonian (Early Downtonian, Ludlow Bone Bed and Downton Castle Sandstone), Shropshire and Herefordshire, England.

*Diagnosis.*—The length of the dorsal shield ranges between 38 and 45 mm., and its width between 26 and 38 mm. There are about 5 dentine ridges per millimeter.

**Cyathaspis acadica** (Matthew). Figure 111.

*Pteraspis* (?) *acadica* Matthew, 1886, Canadian Rec. Sci., **2**, pp. 251–252, 1 fig.

*Diplaspis acadica* Matthew 1887, Bull. Nat. Hist. Soc. New Brunswick, no. **6**, pp. 69–73, 1 fig.; 1888, Trans. Roy. Soc. Canada, **6**, sec. 4. pp. 49–52, pl. 4, figs. 1–4; Claypole, 1892, Quart. Jour. Geol. Soc. London, **48**, p. 547.

*Cyathaspis acadica* Woodward, 1891, Cat. Fossil Fishes Brit. Mus. (Nat. Hist.), **2**, p. 173; Hay, 1902, Bull. U. S. Geol. Surv., **179**, p. 340; 1929, Carnegie Inst. Washington, Publ. **390**, vol. 1, p. 635; Kiaer and Heintz, 1935, Skr. Svalbard Ishavet, **40**, p. 34.

*Type.*—Royal Ontario Museum 1117, incomplete but associated dorsal and ventral shields (fig. 111), originally figured by Matthew (1888, pl. 4, figs. 1–4).

*Occurrence.*—Late Silurian, Jones Creek formation,[1] Cunningham Brook, near Nerepis, Kings County, New Brunswick.

*Diagnosis.*—The size is somewhat smaller than that of *C. banksi.* There are 7 to 8 dentine ridges per millimeter.

*Discussion.*—Matthew (1888, pp. 52–53) recognized that this species was close to *Cyathaspis,* but he referred it to a new genus, *Diplaspis,* because he thought that its "lateral cornua" (=lateral epitega) were divided, and that its "ocular plates" (=supraorbital parts of lateral epitega) were wanting. However, the lateral epitega are formed essentially as in other Cyathaspidinae; their division in the type is the result of breakage, and each does include a supra-

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[1] Listed in error as Long Reach formation by Denison (1956, p. 384); according to the map published by MacKenzie (1951), this is well within the underlying Jones Creek formation.

orbital part (fig. 111). The latter is to be identified as the anterior end with curved ridges of the plates labeled *b* and *b′* in Matthew's figure (1888, pl. 4, fig. 4). In its known characters there is nothing to distinguish this species from *Cyathaspis* and very little to distinguish it from *C. banksi.* The type of ornamentation is precisely the same, with round-topped dentine ridges of two sizes on the central parts of the dorsal and ventral shields (fig. 159,A) and of uniform size elsewhere. The pattern of the ridges is similar also. The pattern of the postrostral field has not been described in *Cyathaspis banksi;* in *C. acadica* the pineal macula is marked by circular ridges around a tubercle (Matthew, 1888, pl. 4, fig. 2), and in front of it ridges radiate toward the rostral epitegum. The ventral shield is surrounded anteriorly and laterally by a band of uniform-sized ridges; Matthew (1888, p. 51) described an anterior triangular area of irregular ridges on it, comparable to the postrostral field of the dorsal shield; this area is not now preserved on the type nor is it recognizable on Matthew's figures. It is possible that the fragment *e* of Matthew's figure (1888, pl. 4, fig. 1) represents part of a branchial plate; this part of the type is no longer preserved. The shape, proportions, and size of *C. acadica* cannot be accurately determined from material available at present.

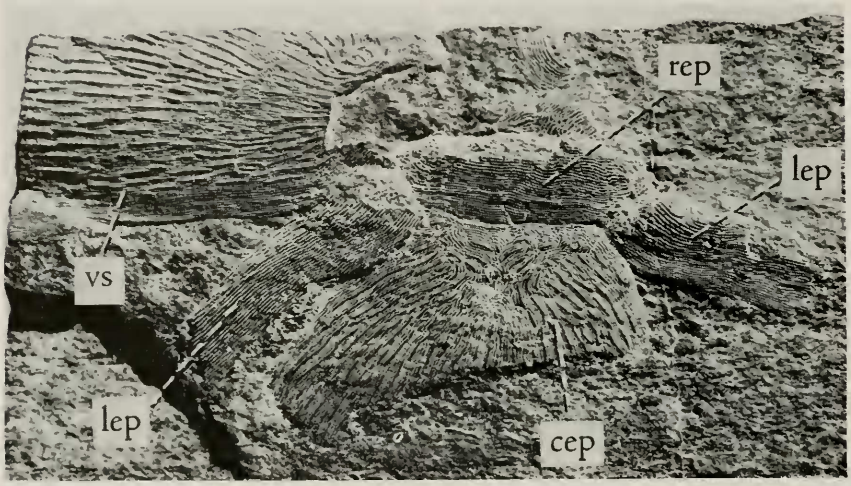

FIG. 111. *Cyathaspis acadica,* type, parts of dorsal and ventral shields; Royal Ontario Museum 1117 (× 5/2).

*cep,* central epitegum; *lep,* lateral epitegum; *rep,* rostral epitegum; *vs,* ventral shield.

During the process of preservation, the type specimen has not only been flattened, but has also been broken into separate parts. The disarticulation of the ventral shield and branchial plates is not remarkable, since this has occurred in nearly all known specimens of cyathaspids. However, the elements of the dorsal shield—the rostral, lateral, and central epitega—are also separated in the type. This is the result of crushing, but the breaks have taken place between the epitega, at what are presumably lines of weakness. Kiaer and Heintz (1935, p. 34) concluded that the shield consisted of "several wholly isolated portions," that is, of separate plates, and this specimen is support for this view.

In Chicago Natural History Museum there are two specimens from the type locality that probably belong to this species. They differ from the type in having generally coarser dentine ridges (5–6 per mm.). PF 1799 is a fragment of the anterior part of a ventral shield showing coarser and finer ridges over much of its surface. Its ridge pattern shows the convergence of the anterior part of the elliptical central pattern, and most anteriorly a divergence or radiation, unsymmetrically developed; there is no indication of an anterior band of transverse ridges. PF 1800 is probably a complete *Cyathaspis* cf. *acadica* contained in a coprolite. This is spread over an oval area about 40 by 50 mm. parallel to the bedding, and contains a crowded mass of scales and plate fragments. A shield fragment about 5 mm. wide covered with uniform (5 per mm.) straight ridges probably belongs to a lateral epitegum. Fragments, presumably from the central epitegum or ventral shield, display the typical coarser and finer ridges. Other shield fragments, possibly from the postrostral field, the lateral part of the rostral epitegum, or the anterior part of the ventral shield show a local subdivision of the ridges into short lengths or into denticles. A long narrow ridge scale is covered with finer (6–7 per mm.), high-crested ridges. Other smaller scales have broader ridges with lower crests. A thin section (fig. 159,A) shows this to be a juvenile specimen, with the reticular, cancellous, and basal layers not yet formed.

### **Cyathaspis(?) miroshnikovi** Obruchev

*Cyathaspis miroshnikovi* Obruchev, 1958, Sovietskaya Geologiya, 1958, no. 11, p. 43 (nomen nudum).

*Occurrence.*—Early Devonian (lower Zubova horizon), near Norilsk, Nats. Okrug, Krasnoyarskiy Territory, Siberia.

### Cyathaspis sp.

*Cyathaspis* sp. ind. Obruchev, 1938, Central Geol. & Prosp. Inst., Mater., Gen. Ser., **2**, pp. 36–38, 42, pl. 1, fig. 1; 1958, Sovietskaya Geologiya, 1958, no. 11, p. 40.

*Occurrence.*—Silurian (?Wenlockian), River Siren-gupan, Basin of River Belaya, southern Urals, USSR.

*Discussion.*—This is based on a shield fragment showing dentine ridges of two sizes, coarser ones separated by three finer ones. Anteriorly there is an area ornamented with small denticles. The reference to *Cyathaspis* is not certain.

### Archegonaspis Jaekel

*Type-species.*—*Cyathaspis* (*Pteraspis*) *integer* Kunth.

*Pteraspis* (in part) Salter, 1859, Ann. Mag. Nat. Hist., (3), **4**, pp. 44–55.

*Scaphaspis* (in part) Lankester, 1868, Fishes Old Red Sandstone, Mon. Pal. Soc., p. 25.

*Cyathaspis* (in part) Kunth, 1872, Zeits. Deutsch. Geol. Ges., **24**, pp. 1–8; Geinitz, 1884, Zeits. Deutsch. Geol. Ges., **36**, pp. 855–857; von Alth, 1886, Beitr. Pal. Geol. Österr.-Ung., **5**, Heft 3, pp. 63–69, 72–73; Woodward, 1891, Cat. Fossil Fishes Brit. Mus. (Nat. Hist.), **2**, p. 173; Lindström, 1895, Bihang K. Svensk. Vetensk.-Akad. Handl., **21**, Afd. 4, Nr. 3, pp. 1–10; Kiaer and Heintz, 1935, Skr. Svalbard Ishavet, **40**, pp. 36–37.

*Palaeaspis* (in part) Jaekel 1911, Die Wirbeltiere, pp. 32–33.

*Archegonaspis* Jaekel, 1927, Zool. Anz., **70**, p. 282; 1927, Zeits. gesamte Anat., Abt. 3, Ergeb. Anat. Entwickl., **27**, pp. 854, 877, 927; 1928, Pal. Zeits., **9**, p. 260; Kiaer, 1932, Skr. Svalbard Ishavet, **52**, pp. 22–23; Heintz, 1933, Zeits. Geschiebeforsch., **9**, pp. 125–130; Flower and Wayland-Smith, 1952, Bull. Mus. Comp. Zool., **107**, pp. 365–366; Denison, 1953, Fieldiana: Geol., **11**, no. 7, pp. 292–293; Stensiö, 1958, Traité de Zool., **13**, fasc. 1, pp. 307–314, 384, 386, 389, 393; Denison, 1963, Fieldiana: Geol., **14**, no. 7, pp. 108, 113, 140.

*Aequiarchegonaspis* Stensiö, 1958, Traité de Zool., **13**, fasc. 1, pp. 307, 308, 310–315.

*Lauaspis* Stensiö, 1958, Traité de Zool., **13**, fasc. 1, pp. 307–316, 319.

*Diagnosis.*—The shields are of moderately broad proportions (width ratio=.61–.62). The orbits and pineal organ are placed more posteriorly than in most *Vernonaspis* (orbital ratio=.13–.16; pineal ratio=.23–.26). There is no median rostral process (fig. 113), but the preorbital processes are well developed. The postbranchial lobes are small. The posterior edge of the shield is nearly transverse. There are 4–5 dentine ridges per millimeter, most of them round-topped. The ridge pattern is transverse on the rostrum. The postrostral field has a fanned or irregular pattern with the ridges occurring as short lengths or denticles. On the ventral shield the pattern is longitudinal, with an anterior area of fanned ridges.

### **Archegonaspis integra** (Kunth)

*Cyathaspis* (*Pteraspis*) *integer* Kunth, 1872, Zeits. Deutsch. Geol. Ges., **24**, pp. 3–7, pl. 1, figs. 1–6.

"*Pteraspis*" *integra* Lindström, 1895, Bihang K. Svensk. Vetensk.-Akad. Handl., **21**, Afd. 4, no. 3, p. 9.

*Cyathaspis integer* Lankester, 1873, Geol. Mag., **10**, p. 243; Jentzsch, 1879, Zeits. Deutsch. Geol. Ges., **31**, p. 793; Roemer, 1885, Palaeont. Abh., **2**, pp. 131–132, pl. 10, fig. 1; von Alth, 1886, Beitr. Pal. Geol. Österr.-Ung., **5**, Heft 3, pp. 65, 73; Woodward, 1891, Cat. Fossil Fishes Brit. Mus. (Nat. Hist.), **2**, p. 173; Leriche, 1906, Mém. Soc. Géol. Nord, **5**, p. 24; Jaekel, 1927, Pal. Zeits., **8**, pp. 177–180, fig. 5; Stensiö, 1927, Skr. Svalbard Nordishavet, **12**, p. 317, fig. 87.

*Palaespis integer* Jaekel, 1911, Die Wirbeltiere, figs. 15, 17.

*Archegonaspis integer* Jaekel, 1927, Zool. Anz., **70**, p. 282, fig. 4; 1927, Zeits. gesamte Anat., Abt. 3, Ergeb. Anat. Entwickl., **27**, p. 854, 927, figs. 14, 54; 1928, Pal. Zeits., **9**, pp. 177–179, fig. 5; Kiaer, 1932, Skr. Svalbard Ishavet, **52**, pp. 23–24, pl. 9, fig. 2; Heintz, 1933, Zeits. Geschiebeforsch., **9**, pp. 127–130, fig. 2; Stensiö, 1958, Traité de Zool., **13**, fasc. 1, p. 310, fig. 173 A, B, 202.

*Type.*—Partially articulated dorsal and ventral shields, branchial plates and scales, figured by Kunth.

*Occurrence.*—Late Silurian (Early Ludlovian), glacial erratics of Graptolithengestein, Schöneberg in Berlin, Germany; also Bydgoszcz (Bromberg), Poland.

*Diagnosis.*—The length of the dorsal shield is about 41 mm. On the central epitegum a few of the ridges stand slightly higher than the others.

### **Archegonaspis lindstromi** Kiaer. Figures 100,B, 112.

*Cyathaspis* cf. *schmidti* Lindström, 1895, Bihang K. Svensk. Vetensk.-Akad. Handl., **21**, Afd. 4, no. 3, pp. 1–10, fig. 1, pls. 1–2; Leriche, 1906, Mém. Soc. Géol. Nord, **5**, p. 23.

*Archegonaspis lindstrømi* Kiaer, 1932, Skr. Svalbard Ishavet, **52**, pp. 23–24, pl. 9, fig.1; Flower and Wayland-Smith, 1952, Bull. Mus. Comp. Zool., **107**, p. 366.

*Archegonaspis lindströmi* Heintz, 1933, Zeits. Geschiebeforsch., **9**, pp. 130–131, fig. 3; Spjeldnaes, 1950, Ark. Min. Geol., **1**, Nr. 8, p. 213; Ørvig, 1951, Ark. Zool., (2), **2**, No. 2, fig. 5B.

*Cyathaspis lindströmi* Kiaer and Heintz, 1935, Skr. Svalbard Ishavet, **40**, pp. 36–37.

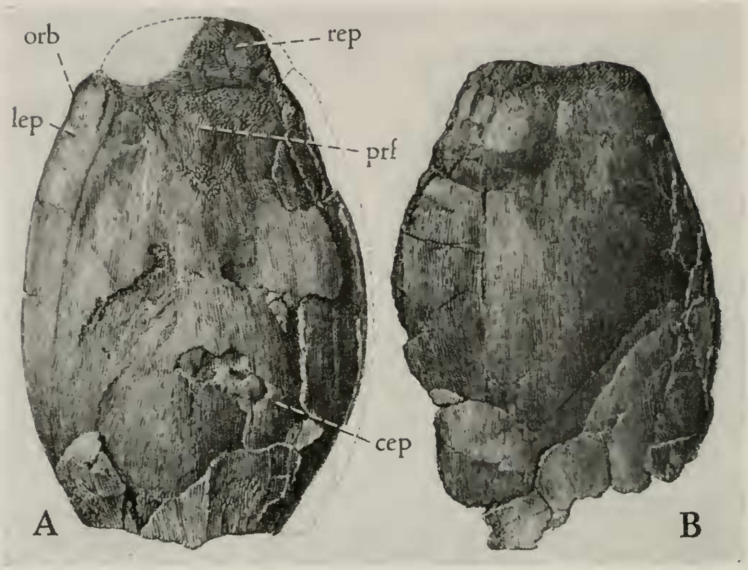

FIG. 112. *Archegonaspis lindstromi*, type (from Lindström, 1895); Stockholm, Naturhistoriska Riksmuseet, C 1564 (× 3/2). A, dorsal shield; B, ventral shield. *cep*, central epitegum; *lep*, lateral epitegum; *orb*, orbit; *prf*, postrostral field; *rep*, rostral epitegum.

*Lauaspis lindströmi* Stensiö, 1958, Traité de Zool., **13**, fasc. 1, p. 307, figs. 172A,B.

*Type.*—Associated dorsal and ventral shields, Naturhistoriska Riksmuseet, Stockholm, C 1564.

*Occurrence.*—Late Silurian (Early Ludlovian), Marl Shales of Hemse Group, Lau Canal, Gotland, Sweden.[1]

*Diagnosis.*—The length of the dorsal shield is 47 mm., and that of the ventral shield is 44 mm. The dentine ridges are strongly convex and of uniform size. The shields of the type appear somewhat broader than those of other species as a result of crushing.

### Archegonaspis cf. lindstromi

*Onchus windti* Weigelt, 1930, Zeits. Geschiebeforsch., **6**, pp. 6–10.

*Archegonaspis* cf. *lindströmi* Heintz, 1933, Zeits. Geschiebeforsch. **9**, pp. 130–131, fig. 1.

*Type.*—Associated branchial plates and scales; Heimatmuseum at Köthen, Germany.

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[1] Listed in error from Skåne, south Sweden by Kiaer (1932, p. 23).

*Occurrence.*—Late Silurian (Early Ludlovian), glacial erratic of Graptolithengestein, Müntzeschen quarry, Köthen, Saxony, Germany.

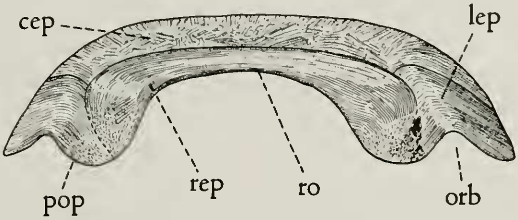

FIG. 113. *Archegonaspis schmidti*, rostral view, drawn from cast of type specimen (× 3).

*cep*, central epitegum; *lep*, lateral epitegum; *orb*, orbit; *pop*, preorbital process; *rep*, rostral epitegum; *ro*, rostrum.

### **Archegonaspis ludensis** (Salter)

*Pteraspis ludensis* Salter, 1859, Ann. Mag. Nat. Hist., (3), **4**, pp. 45–47, fig. 1.

*Scaphaspis ludensis* Lankester, 1868, Fishes Old Red Sandstone, Mon. Pal. Soc., p. 25, pl. 2, figs. 4, 4*a*.

*Cyathaspis ludensis* Woodward, 1891, Cat. Fossil Fishes Brit. Mus. (Nat. Hist.), **2**, p. 173.

*Archegonaspis ludensis* Kiaer, 1932, Skr. Svalbard Ishavet, **52**, p. 24; White, 1958, Studies on Fossil Vertebrates, Westoll ed., p. 218.

*Type.*—Ventral shield, Geological Survey and Museum, London, 49106.

*Occurrence.*—Late Silurian (Middle Ludlovian), highest Lower Leintwardine beds, (according to Dr. J. D. Lawson, in litt.) Church Hill, Leintwardine, Herefordshire, England.

*Diagnosis.*—The length of the ventral shield is about 38 mm. The dentine ridges are of uniform size. The reference of this species to *Archegonaspis* is not firmly established.

### **Archegonaspis schmidti** (Geinitz). Figure 113.

*Cyathaspis schmidti* Geinitz, 1884, Zeits. Deutsch. Geol. Ges., **36**, pp. 854–857, pl. 30; Roemer, 1885, Palaeont. Abh., **2**, p. 132.

(?)*Cyathaspis schmidti* Woodward, 1891, Cat. Fossil Fishes Brit. Mus. (Nat. Hist.), **2**, p. 173.

*Archegonaspis integer* var. *schmidti* Kiaer, 1932, Skr. Svalbard Ishavet, **52**, p. 24.

*Aequiarchegonaspis schmidti* Stensiö, 1958, Traité de Zool., **13**, fasc. 1, p. 307, fig. 174.

*Type.*—Dorsal shield, Rostock University Museum (fide Woodward, 1891).

*Occurrence.*—Late Silurian (Early Ludlovian), glacial erratic of Graptolithengestein, Rostock, northern Germany.

*Diagnosis.*—The length of the dorsal shield is 38 mm. The dentine ridges are of uniform size, and perhaps less strongly convex than in *A. integra* and *A. lindstromi.*

### **Archegonaspis** sp.

*Archegonaspis* sp. White, 1958, Studies on Fossil Vertebrates, Westoll ed., p. 218.

*Occurrence.*—Late Silurian (Middle Ludlovian) and (?)Early Devonian (Bone Bed), Radnorshire, Wales.

### **Seretaspis** Stensiö

*Type-species.*—*Seretaspis zychi* Stensiö.

*Seretaspis* Stensiö, 1958, Traité de Zool., **13**, fasc. 1, pp. 314, 315, 316, 318, 366, 371, 384, 386, 387, 391, 393.

*Diagnosis.*—*Seretaspis* resembles *Archegonaspis* in most of its known characteristics. Its epitega, including the postrostral field, are clearly distinct. Its dentine ridges are long and of quite uniform size. There is a slight median convexity, but no lobe, on the rostral border. The dentine ridges are very fine.

### **Seretaspis zychi** Stensiö

*Seretaspis zychi* Stensiö, 1958, Traité de Zool., **13**, fasc. 1, fig. 204.

*Type.*—Naturhistoriska Riksmuseet, Stockholm, C 1608*a*, *b*, incomplete dorsal shield in counterpart.

*Occurrence.*—Early Devonian (Gedinnian), presumably Czortków stage (labeled "Downtonian"), Podolia.

*Diagnosis.*—The length of the dorsal shield is not known, but its maximum width is estimated to have been 18.5 mm., and its pineal length is 8.8 mm. There are 8–9 dentine ridges per millimeter, and their crowns are gently convex, or sharp-crested near the lateral border.

*Discussion.*—Stensiö (1958, p. 366, fig. 204) considered *Seretaspis* to be related to *Anglaspis.* Its most striking characteristics, as interpreted by him, and its presumed similarities to *Anglaspis*, are related to the shortness of the dorsal shield posteriorly. The latter results in a relatively small number of gill pouches and gill arches, and in a posterior position for the branchial openings. However, the type and only specimen of *Seretaspis zychi* is clearly incomplete posteriorly; this is suggested by the asymmetry of the posterior edge shown in Stensiö's figure, and is clearly demonstrated by the counterpart of this specimen. Thus there is no way to determine the length or proportions of the dorsal shield, or to count the number of gill pouches and gill arches. In addition, it is probable that the external branchial openings lay just posterior to the preserved part of the shield, that there were the usual postbranchial lobes behind them, and that *Seretaspis* was not strikingly different from typical cyathaspids in the position of these openings.

As far as it is known, the pattern of the dentine ridges is typical of the Cyathaspidinae. On the rostral epitegum the anterior ridges are parallel to the anterior edge and thus more or less transverse. More posterior rostral ridges radiate from a median point on the epitegum's posterior border, and are thus antero-posteriorly directed centrally, and nearly transverse laterally near the posterior edge. The ridges of the postrostral field radiate from the pineal macula, except for one or two ridges that run parallel to the anterior edge of the field. Little is shown of the pattern of the central epitegum, and minor irregularities make it difficult to determine whether the overall pattern is longitudinal or elliptical. On the lateral epitega, the ridges curve over the orbits, are irregular or diagonal behind the orbits, and are longitudinal posteriorly. Little of the lateral lines can be determined. The pores are large and are commonly encircled by a ridge. There is no suggestion of the branchings and irregularities that typify the Irregulareaspidinae.

The known characteristics of *Seretaspis* show little to distinguish it from *Archegonaspis*. It is considerably younger than known species of *Archegonaspis*, and has much finer ridges. This is hardly enough for generic distinction, but *Seretaspis* is provisionally retained as distinct, pending the discovery of more complete material.

### **Vernonaspis** Flower and Wayland-Smith

*Type-species.—Vernonaspis allenae* Flower and Wayland-Smith.

*Cyathaspis* (in part) Bryant, 1926, Proc. Amer. Phil. Soc., **65**, pp. 266–270.

*Eoarchegonaspis* (nomen nudum) Kiaer, 1932, Skr. Svalbard Ishavet, **52**, p. 24.

*Vernonaspis* Flower and Wayland-Smith, 1952, Bull. Mus. Comp. Zool., **107**, pp. 373–374; Stensiö, 1958, Traité de Zool., **13**, fasc. 1, pp. 307, 312–315, 319; Denison, 1963, Fieldiana: Geol., **14**, no. 7, pp. 108–109, 113, 140.

*Diagnosis.*—The shields are moderately broad to narrow (width ratio of dorsal shield=.54–.64. The orbits and pineal organ are typically forward in position (orbital ratio=.10–.14; pineal ratio=.20–.22 or more). The postbranchial lobes are long (postbranchial ratio=.34–.45), but their development is weak to moderate. The preorbital processes and the median lobe on the rostral edge of the dorsal shield are strongly developed. The dentine ridges are fine to moderately coarse (5–9 per mm.); they usually have a gently convex crown, though they may be flat-topped anteriorly and sharply crested at the lateral margins of the dorsal shield behind the orbits. The rostral epitegum is clearly marked, usually with ridges arranged in part transversely. The postrostral field is not distinct from the central epitegum.

*Discussion.*—*Vernonaspis* appears to be widespread and common in the Late Silurian rocks of North America. It is most closely similar to the contemporary European genus, *Archegonaspis*, from which it differs in the following characters: its shield is usually narrower; its orbits and pineal organ are usually more anterior; its dentine ridges are usually finer; it has a well-developed medial rostral process (figs. 117,A, 123,C) and its postrostral field is not distinct from the central epitegum.

Differentiation of species in *Vernonaspis* is difficult. The ridge pattern, which is one of the most obvious features, shows great variation in detail and for this reason cannot be relied on entirely. Shape and proportions are rarely accurately determinable because of incompleteness and crushing of specimens. The species have been distinguished rather arbitrarily, mostly on the basis of size and on the coarseness of ridges. It has been found that two species commonly occur together, one of them larger and with coarser ridges, and the other smaller and with finer ridges; in each of two localities three species have been determined.

### **Vernonaspis allenae** Flower and Wayland-Smith. Figure 114.

*Vernonaspis allenae* Flower and Wayland-Smith, 1952, Bull. Mus. Comp. Zool., **107**, pp. 375–376, pl. 1, pl. 2, figs. 3, 8.

*Vernonaspis leonardi* (in part) Flower and Wayland-Smith, Bull. Mus. Comp. Zool., **107**, pl. 2, figs. 6–7, pl. 5, fig. 2.

cf. *Vernonaspis leonardi* Flower and Wayland-Smith, Bull. Mus. Comp. Zool., **107**, pp. 378–380, pl. 3, figs. 2–4, pl. 4, pl. 5, fig. 1.

*Type.*—Museum of Comparative Zoology 8871 (fig. 114), a dorsal shield figured by Flower and Wayland-Smith (1952, pl. 1., pl. 2., figs, 3, 8).

FIG. 114. *Vernonaspis allenae,* photograph of rubber impression of type dorsal shield; Museum of Comparative Zoology 8871 (× 3).

*Referred specimens.*—Mus. Comp. Zool. 8873, a ventral shield, and 8874, a dorsal shield.

*Occurrence.*—Late Silurian, Vernon shale (Salina group), 2 miles southeast of Kenwood, Oneida County, New York.

Doubtfully from the Wills Creek formation, cut on Western Maryland Railroad at Round Top, near Hancock, Maryland.

*Diagnosis.*—The length of the dorsal shield is 32–33 mm. There are 6–7 dentine ridges per millimeter. The dorsal shield usually has a rounded median lobe on its posterior edge. It is rather narrow, with a width ratio of .54–.57.

*Discussion.*—The ridge pattern of the type (fig. 114) is as follows: On the rostral epitegum 3 ridges are parallel to the anterior edge; the posterior ridges are transverse but curve forward toward the sides to follow the posterior edge of the epitegum, and the central ridges are fanned or radiate toward the front. The ridges of the postrostral field radiate fan-wise from the pineal organ, then curve laterally and backward into the longitudinal ridges of the central epitegum. The latter are arranged somewhat sinuously and slightly elliptically.

The ventral shield referred by Flower and Wayland-Smith to *V. leonardi* (Mus. Comp. Zool. 8873) has an estimated length of 26 mm., which is about what it should be in *V. allenae,* and there are 6 ridges per millimeter, as in the latter. The posterior edge has an obtuse median angle. The ridge pattern is essentially longitudinal, but the anterior ridges radiate toward the antero-lateral corners, and there appear to be about 4 ridges that may extend transversely across the anterior end. The fine cracks and ridges on the inner surface have nothing to do with the lateral line system as believed by Flower and Wayland-Smith (1952, fig. 1).

The dorsal shield in counterpart referred by Flower and Wayland-Smith to cf. *Vernonaspis leonardi* (Mus. Comp. Zool. 8874) is also referred to *V. allenae.* Its length is 33.5 mm., about as in the type of *V. allenae,* and there are about 6 dentine ridges per millimeter. It is considerably broader than the type of *V. allenae,* but this is attributable to flattening.

Less certainly referable to *Vernonaspis allenae* are specimens from the Wills Creek formation at Round Top, near Hancock, Maryland. Four poorly preserved dorsal shields collected by J. R. Beerbower (CNHM, PF 3650–3653) agree in size, proportions, and in coarseness of ridges. One of these (PF 3650), but apparently not all, differs from the usual *Vernonaspis* situation in having all of the rostral ridges transverse. A ventral shield (CNHM, PF 2156) collected by Willard P. Leutze at the same locality agrees in size and ridge coarseness, but differs from known *Vernonaspis* in the somewhat uneven ridge width, the prominence of the lateral line pores, and in having an unornamented brim along the sides and around the antero-lateral corners.

### **Vernonaspis leonardi** Flower and Wayland-Smith. Figure 115.

*Vernonaspis leonardi* (in part) Flower and Wayland-Smith, 1952, Bull. Mus. Comp. Zool., **107**, pp. 376–378, pl. 3, fig. 5.

*Type.*—This was not specifically designated by Flower and Wayland-Smith, but their description was based primarily on a dorsal shield, now Museum of Comparative Zoology 8872 (fig. 115), which is here named lectotype.

*Occurrence.*—Late Silurian, Vernon shale (Salina group), 2 miles southeast of Kenwood, Oneida County, New York (the lectotype).

Late Silurian, High Falls formation, east side of Route 23, 0.9 miles (1.4 by road) south-southeast of Duttonville, Montague township, Sussex County, New Jersey (CNHM, PF 840, 844, 846).

FIG. 115. *Vernonaspis leonardi*, photograph of rubber impression of anterior part of type dorsal shield (from Flower and Wayland-Smith, 1952); Museum of Comparative Zoology 8872 (× 4).

Also from High Falls formation, cut on Delaware Water Gap–Millbrook road, opposite Shawnee Island, Warren County, New Jersey (CNHM PF 861).

*Diagnosis.*—The length of the dorsal shield is 27–29 mm. The dentine ridges are very fine, 7½–9 per mm. The shield is moderately narrow, with a width ratio of .54.

*Discussion.*—This species is smaller than *V. allenae* and about the size of *V. vaningeni*, but has much finer dentine ridges than either. The gently convex crowns of the dentine ridges of the referred specimens are typical of *Vernonaspis*, but in the type they are flat, with a faint, narrow ridge centered on the crest; this peculiarity is believed to be the result of crushing. Flower and Wayland-Smith distinguished *V. leonardi* from *V. allenae* by shape (but this is incomplete and altered by crushing), by smaller pustules on the surface (a peculiarity of preservation), by the thicker cancellous layer (a difference I cannot observe), and by the arrangement of the ridges in whorls extending from the pineal organ (but the pattern is much as described above in *V. allenae*).

Three specimens from Montague township, New Jersey (CNHM, PF 840, 844, and 846) show close agreement with the typical *V. leonardi*. One specimen from near Delaware Water Gap, New Jersey (CNHM, PF 861) shows parts of three dorsal shields of about the size of *V. leonardi* and with very fine ridges. Epitega are distinct except for the postrostral field, and in one dorsal shield the central ridges continue longitudinally through the postrostral field.

**Vernonaspis vaningeni** (Bryant). Figures 116–118.

*Phyllocarida* (in part) Clarke, 1907, Bull. N. Y. State Mus., **107**, p. 310, pl. 8, figs. 14–17.

*Anatifopsis wardelli* (in part) Ruedemann, 1916, Bull. N. Y. State Mus., **189**, pp. 102–105, pl. 32, figs. 1, 9, 11.

*Cyathaspis van ingeni* Bryant, 1926, Proc. Amer. Phil. Soc., **65**, pp. 269–270, pl. 2, fig. 1, pl. 4, fig. 2; Flower and Wayland-Smith, 1952, Bull. Mus. Comp. Zool., **107**, pp. 366–370.

*Cyathaspis wardelli* (in part) Bryant, 1926, Proc. Amer. Phil. Soc., **65**, pp. 266–269, pl. 2, figs. 5–6.

*Eoarchegonaspis* (nomen nudum) *wardelli* Kiaer, 1932, Skr. Svalbard Ishavet, **52**, p. 24, fig. 12.

*Archegonaspis van ingeni* Beerbower and Hait, 1959, Proc. Pennsylvania Acad. Sci., **33**, p. 203, fig. 2.

*Lectotype.*—Bryant did not designate a type in his original description, but Princeton 12916 (fig. 116) is marked as type and is hereby so named. It is an incomplete dorsal shield, figured by Bryant (1926, pl. 2, fig. 1).

*Occurrence.*—The material studied by Clarke, Ruedemann, and Bryant all came from near Otisville, Orange County, New York, but the precise localities and horizons are difficult to determine. Cyathaspididae have been found in three localities along the Erie Railroad tracks in this vicinity. One of these, at Shin Hollow, is clearly in the Longwood shale and contains *Americaspis, Vernonaspis* sp., and undetermined cyathaspids. The material described by Clarke (1907) probably came from the same locality as that described by Ruedemann (1916). Both lots were collected by H. C. Wardell and are lithologically similar—greenish-gray siltstones with brown iron stains. Clarke gives the horizon as "gray shales above the grit" in the upper part of the Shawangunk formation, while Ruedemann says his specimens came from "a bed of greenish shaly sandstone above the eurypterid-bearing strata." The horizon is the upper member of the Shawangunk formation, named the Otisville Shale member by Swartz and Swartz (1931, p. 651). It was listed as Guymard Quartzite by Kilfoyle (1954, pp. 499–500), but this name has not been widely used. The precise locality is probably not now determinable. Ruedemann (1916, p. 105) gives it as. ". . . railroad cut north of Otisville, on the eastern slope of Shawangunk Mountain . . ." This is evidently in error as there is no railroad cut north of Otisville and no Shawangunk formation on the eastern slope of the mountain (Kilfoyle, in litt., Dec. 7, 1961). The material probably came from the western slope of the mountain, possibly near the stone crusher which was formerly located about 1¾ miles southwest of Otisville.

The syntypic material (Princeton 12916, 12919–12921) described by Bryant (1926) was collected by Prof. Gilbert Van Ingen of Princeton University. Bryant gives the locality as Guymard, and the specimen labels say either "near Guymard" or "just N. of Guymard." This is in the vicinity of Graham Station on the Erie Railroad as it descends the western slope of Shawangunk Mountain, and is possibly about two miles south of the locality where Clarke's and Ruedemann's material was obtained. The horizon is given as Guymard Quartzite, which is probably equivalent to the Otisville Shale member of the Shawangunk formation. Bryant (1926, pp. 259–260), writing from Van Ingen's notes, says that near its top the Guymard formation contains thin red shales prophetic of the overlying Longwood shale; it was from the lowermost of these red shales (or more properly siltstones) that the material described by Bryant was obtained. The horizon is thus about the same as or perhaps slightly higher than that of Clarke's and Ruedemann's specimens.

Additional localities: High Falls formation, east side of route 23, 0.9 miles (1.4 by road) south-southeast of Duttonville, Montague township, Sussex County, New Jersey (CNHM, PF 847–854, 3340).

Upper Bloomsburg formation, cuts on U. S. highway 611, about 200 yards north of toll station, Delaware River bridge, Monroe County, Pennsylvania (CNHM, PF 3647–3649, collected by J. R. Beerbower).

*Diagnosis.*—The length of the dorsal shield is 26.5–28.5 mm. There are 5½–6½ dentine ridges per millimeter. A median lobe may be absent on the posterior edge of the dorsal shield. The width ratio is about .56.

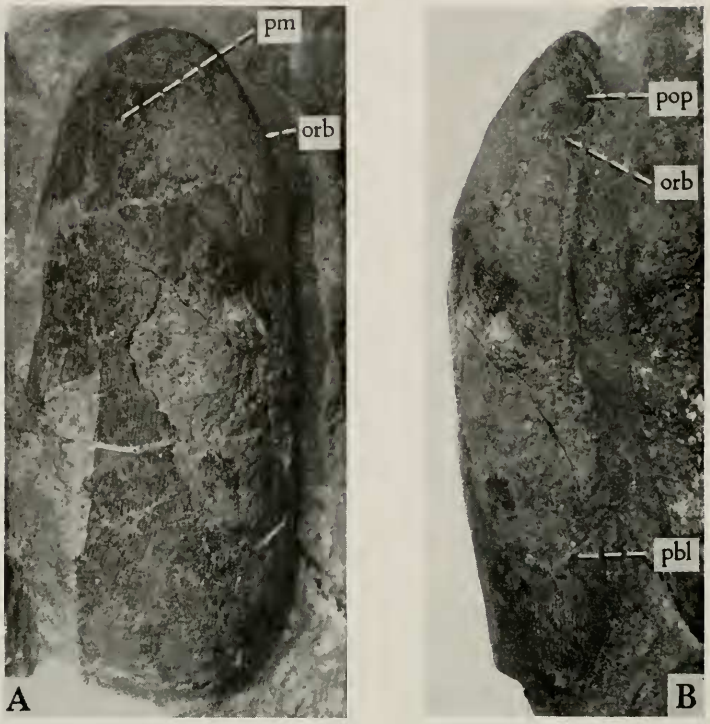

FIG. 116. *Vernonaspis vaningeni*, type; incomplete dorsal shield, Princeton 12916 (× 3). A, dorso-lateral view; B, lateral view of right side.

*orb*, orbit; *pbl*, postbranchial lobe; *pm*, pineal macula; *pop*, preorbital process.

*Discussion.*—The considerable taxonomic confusion that has developed in the history of this species and of "*Cyathaspis*" *wardelli* has been reviewed but not resolved by Flower and Wayland-Smith. The syntypic material of Ruedemann's species, *Anatifopsis wardelli*, comprises the twelve specimens that he figured (1916, pl. 32, figs. 1–12), but he did not designate a holotype. A lectotype was named by Flower and Wayland-Smith, and they intentionally selected an unrecognizable fragment (New York State Mus. 9613). This made future use of the specific name, *wardelli*, impracticable, and also effectively prohibited use of the generic name, *Eoarchegonaspis*, which was based on this species. Since the lectotype of *Anatifopsis wardelli* exhibits no diagnostic characters, the other eleven specimens cannot be identified with it and are available for systematic restudy. In my opinion this suite of specimens includes two species of *Vernonaspis*, as well as some undeterminable fragments. A *Vernonaspis* of smaller size and with finer ridges is described below as a new species, *V. bryanti.* A larger form with broader ridges (New York State Mus. 9612, 9620, 9622, 9624–5, 11470–1) agrees with the species described by Bryant as *Cyathaspis van ingeni.* Bryant also described and figured specimens which he referred to *Cyathaspis wardelli.* The characters by which Bryant distinguished these two species are attributable either to distortion in preservation or to misinterpretation of their structure. *V. vaningeni* was considered to have a narrower shield, but the type (fig. 116) is incomplete and is missing nearly all of the left side posteriorly; if restored it would have a moderately broad shield comparable to that of specimens referred to *C. wardelli.* Besides, the type of *vaningeni* is compressed laterally while most of the specimens that Bryant referred to *wardelli* are compressed dorsoventrally. The differences he mentions in proportion, arching, and depression of the snout may all be attributed to differences in preservation. Therefore, two of the specimens referred by Bryant to *Cyathaspis wardelli* (Princeton 12920–1) are here referred to *Vernonaspis vaningeni,* while another (Princeton 12922) belongs to *V. bryanti.* Kiaer (1932) and Beerbower and Hait (1959) have previously expressed the belief that Bryant's two species were really identical.

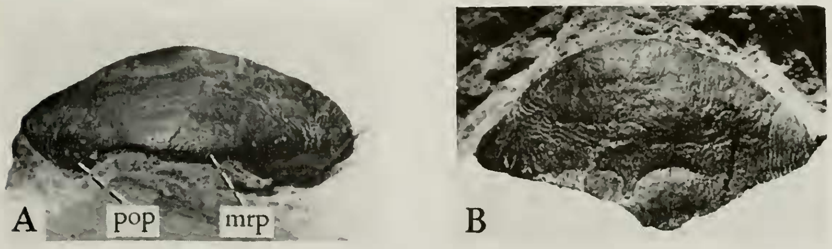

FIG. 117. *Vernonaspis vaningeni,* anterior part of dorsal shield; New York State Museum 9625 (× 4). A, rostral view; B, dorsal view.
*mrp,* median rostral process; *pop,* preorbital process.

This species has the characteristics of *Vernonaspis* as defined above, and is clearly different from *Cyathaspis* and *Archegonaspis.* It is about the size of *V. leonardi* but has coarser ridges. It is smaller than *V. allenae,* with which it agrees in coarseness of ridges. The ridge pattern is similar in general to that described above in *V. allenae* but is variable in detail. The central ridges of the rostral epitegum may be longitudinal, fanned, denticulate (in the type), or irregular (New York State Mus. 11470, 9625, fig. 117). The rostral margin is denticulate in Princeton 12919. A pineal macula, rarely seen in

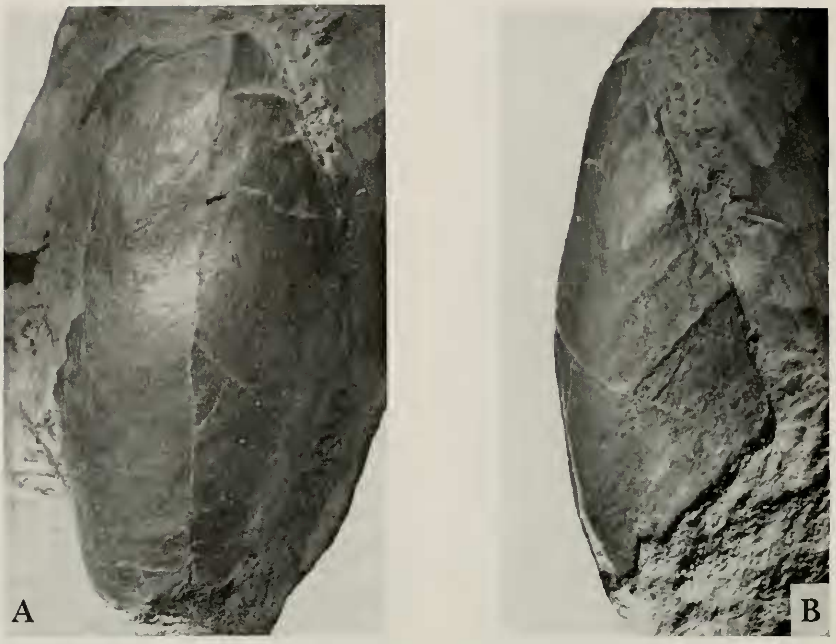

FIG. 118. *Vernonaspis vaningeni*, ventral shield, CNHM, PF 853 (× 3). A, ventral view; B, lateral view of left side.

*Vernonaspis*, consists of an elongate oval of three ridges in the type (fig. 116, *pm*). The ridge pattern of the lateral epitegum is typical of the genus: the ridges curve over the orbit and converge with transverse rostral ridges anteriorly on the preorbital process; behind the orbit a few sharp-crested ridges run parallel to the edge, while medial to them the ridges are arranged diagonally anteriorly and become longitudinal more posteriorly.

The ventral shield (fig. 118) is deeply arched posteriorly, has a small postero-median lobe (CNHM, PF 854), and a median notch on the anterior border (CNHM, PF 853). The dentine ridges are sinuously longitudinal except that they radiate fan-wise at the anterior end, and a few ridges run parallel to the lateral borders.

**Vernonaspis bryanti,** new species. Figures 119–120.

*Phyllocarida* (in part) Clarke, 1907, Bull. N. Y. State Mus., **107**, pl. 8, figs. 20–21.

*Anatifopsis wardelli* (in part) Ruedemann, 1916, Bull. N. Y. State Mus., **189**, pp. 102–105, pl. 32, figs. 3, 6–8.

FIG. 119. *Vernonaspis bryanti*, type; dorsal shield, CNHM, PF 838 (× 4). *lep*, lateral epitegum; *orb*, orbit; *pm*, pineal macula; *rep*, rostral epitegum.

*Cyathaspis wardelli* (in part) Bryant, 1926, Proc. Amer. Phil. Soc., 65, pp. 266–269, pl. 4, fig. 1.

*Type.*—CNHM, PF 838, a nearly complete dorsal shield (fig. 119).

*Occurrence.*—Late Silurian, High Falls formation, east side of New Jersey Highway 23, 0.9 miles (1.4 by road) south-southeast of Duttonville, Montague township, Sussex County, New Jersey (CNHM, PF 838, 839, 841, 842, 845, 855).

Otisville Shale member of Shawangunk formation, near Otisville and Guymard,[1] Orange County, New York (New York State Mus. 9614, 9617–9619, 9626; Princeton 12922, 18004).

Upper Bloomsburg formation, cuts on U. S. Highway 611, about 200 yards north of toll station, Delaware River bridge, Monroe

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[1] See note on this occurrence under *V. vaningeni* (p. 373).

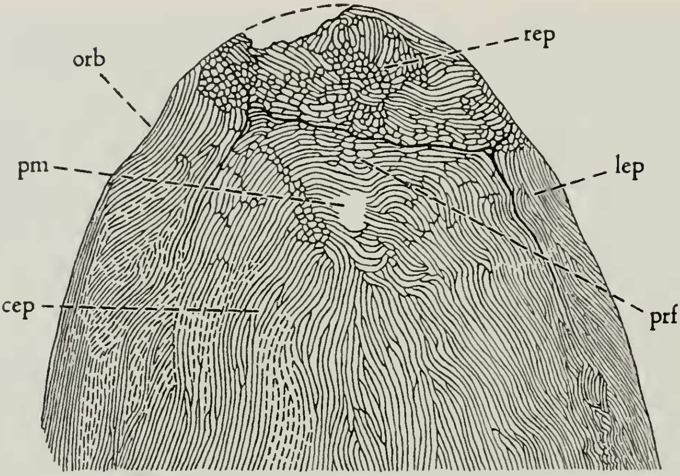

FIG. 120. *Vernonaspis bryanti*, anterior part of type; dorsal shield, CNHM, PF 838 (× 6).

*cep*, central epitegum; *lep*, lateral epitegum; *orb*, orbit; *pm*, position of pineal macula, removed on this specimen; *prf*, postrostral field; *rep*, rostral epitegum.

County, Pennsylvania (CNHM, PF 3646, collected by J. R. Beerbower).

*Diagnosis.*—The length of the dorsal shield is 23–24 mm. Its dentine ridges are very fine, 8–9 per mm. The median lobe on the posterior edge of the dorsal shield is slight or absent. The width ratio is .60–.61.

*Discussion.*—*Vernonaspis bryanti* is the smallest species of the genus, and is distinguished from all except *V. leonardi* by its very fine dentine ridges. It may be identical to the species described by Flower and Wayland-Smith as *Archegonaspis drummondi*, which agrees in its small size and fine ridges. However, as is indicated below (p. 444), the latter does not display characters permitting either generic or specific identification, so identity cannot be proved.

The type dorsal shield is relatively broader than most other *Vernonaspis*, but the breadth may have been increased by crushing. The postbranchial lobe, well shown in the type and in PF 839, is relatively long (postbranchial ratio=.40) but is weakly developed. The ridge pattern is much as in *V. vaningeni* and *V. allenae*, that of the rostral epitegum and postrostral field being quite variable. In the rostral epitegum the central ridge pattern is elliptical in PF 838 (fig. 120), a pair of whorls in PF 839, fanned in Princeton 12922, and irregular and denticulate in New York State Mus. 9617; there

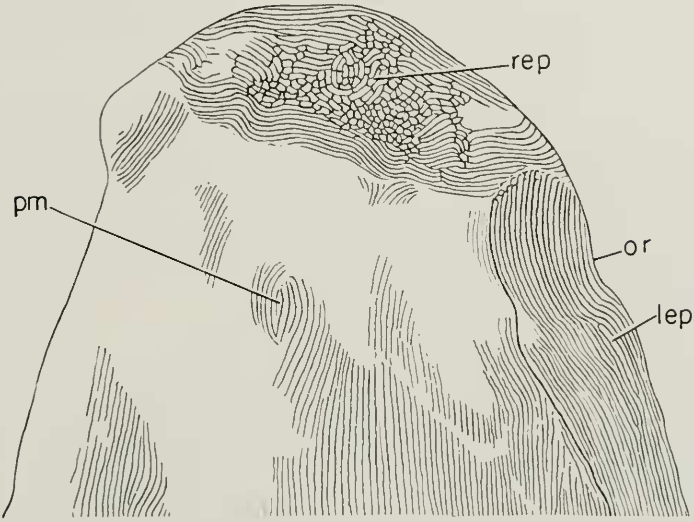

FIG. 121. *Vernonaspis bamberi*, anterior part of dorsal shield of type (from Denison, 1963); Princeton 17081 (× 4).

*lep*, lateral epitegum; *or*, orbit; *pm*, pineal macula; *rep*, rostral epitegum.

are posterior transverse ridges, commonly broken into short lengths, and anterior ridges parallel to the anterior edge. In the postrostral field transverse ridges in the type (fig. 120, *prf*) curve back into longitudinal central ridges; in Princeton 12922 the ridges of the postrostral field are antero-posteriorly and diagonally arranged, and in Princeton 18004 there are irregular convolutions.

In the ventral shields referred here, the dentine ridges are slightly coarser (7–8 per mm.). The anterior edge has a median concavity, and the posterior edge has a slight median lobe in PF 855, though this is absent in PF 3646. The ridges are mainly longitudinal, but radiate anteriorly toward the antero-lateral corners.

One branchial plate (New York State Mus. 9618) is referred here. It is 11.5 mm. long, has a maximum depth of 2.8 mm., and has nearly 10 dentine ridges per millimeter. The ridges are predominantly longitudinal and mostly flat-topped, but are sharp-crested near one edge. This plate is bluntly terminated at the anterior end and tapers toward the posterior end.

**Vernonaspis bamberi** Denison. Figure 121.

*Vernonaspis bamberi* Denison, 1963, Fieldiana: Geol., **14**, no. 7, pp. 110–113, figs. 60–61.

*Type.*—Princeton 17081, a nearly complete though crushed and distorted dorsal shield (fig. 121).

*Referred specimens.*—Princeton 17082–87; 17091.

*Occurrence.*—Probably Early Devonian (Early Downtonian) limestones and graptolitic shales,[1] Beaver River, southeastern Yukon.

*Diagnosis.*—The length of the dorsal shield is 43–46 mm. There are 5–6 dentine ridges per millimeter. The posterior edges of the dorsal and ventral shields are evenly convex, without median lobes. The width ratio is .56.

*Discussion.*—See under *Vernonaspis major.*

**Vernonaspis major** Denison. Figure 122.

*Vernonaspis major* Denison, 1963, Fieldiana: Geol., **14**, no. 7, pp. 110–113, figs. 62–63.

*Type.*—Princeton 17104, a complete dorsal shield (fig. 122).

*Referred specimens.*—Princeton 17105–07, 17376.

*Occurrence.*—Same as *V. bamberi.*

*Diagnosis.*—The length of the dorsal shield is 57 mm. There are 5–6 dentine ridges per millimeter. The dorsal shield has a rounded median lobe on its posterior edge.

*Discussion.*—The two species from the Yukon are larger than the species from the northeastern United States but are in most respects typical members of the genus. Both commonly have circular ridges around the pores of the supraorbital canal (fig. 122, *soc*). *V. major,* especially, shows a tendency to fragmentation of the rostral ridges, and in the type (fig. 122, *rep*) the anterior part is denticulate, even the ridges that usually run parallel to the anterior edge are present only as denticles. As in other *Vernonaspis* the pineal organ is usually not marked by any ridge pattern, though there is commonly a small elevation at this point. The ridge pattern of the postrostral field is variable: in the type of *V. major* the ridges extend a short distance anteriorly from the pineal elevation, curve laterally, then curve backward into the longitudinal ridges of the central epitegum; in another specimen (17106) the ridges of the central epitegum continue longitudinally through the postrostral field to meet the transverse ridges of the rostral epitegum. In *V. major* the postbranchial lobes appear to be more strongly developed than in other *Vernonaspis,* and are

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[1] Tentatively assigned to the Middle Ludlovian in Denison (1963); see below (pp. 450–451).

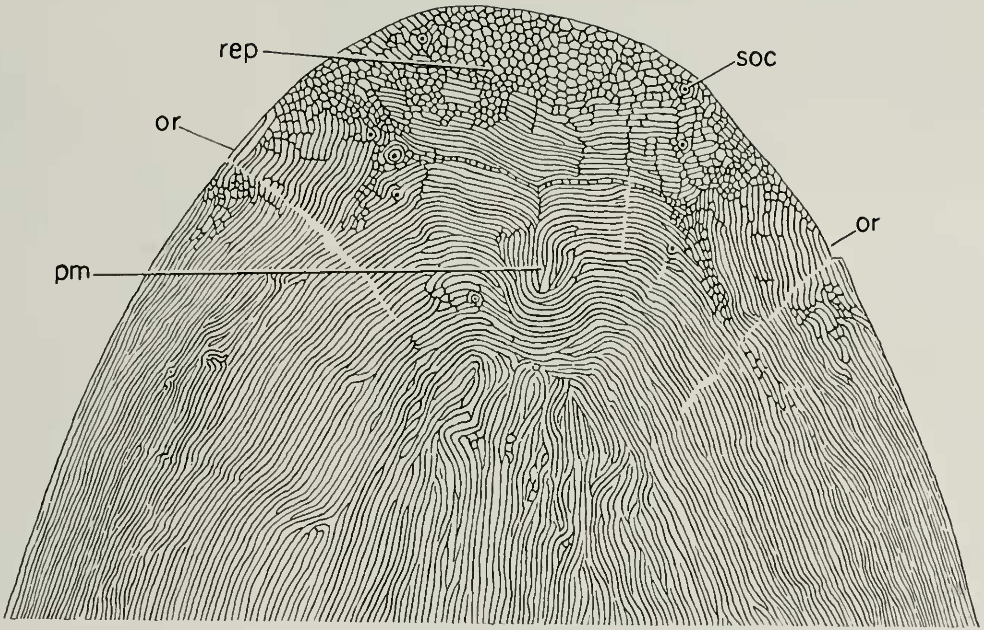

FIG. 122. *Vernonaspis major*, anterior part of dorsal shield of type (from Denison, 1963); Princeton 17104 ( × 4). *or*, orbit; *pm*, pineal region; *rep*, rostral epitegum; *soc*, pores of supraorbital sensory canal.

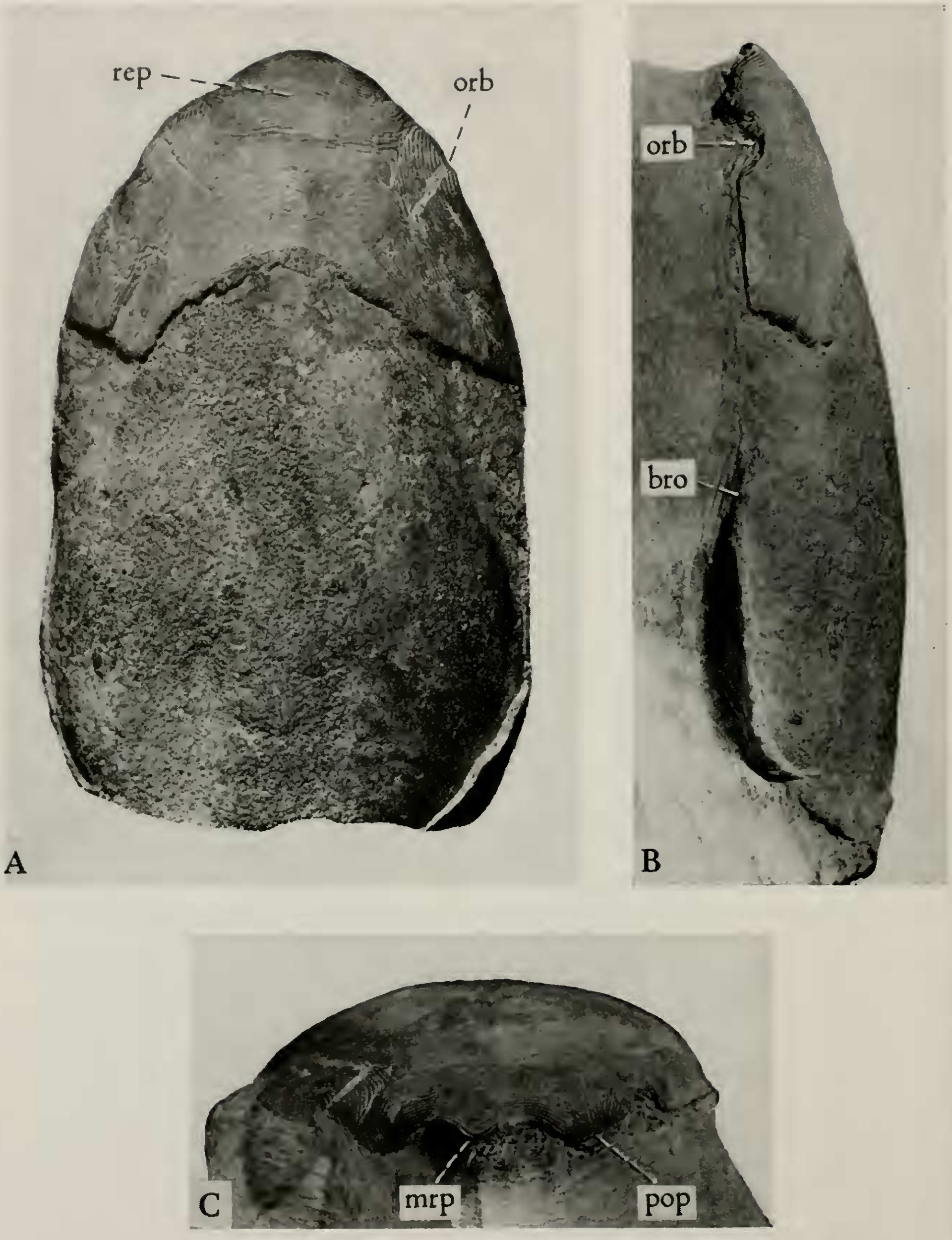

Fig. 123. *Vernonaspis sekwiae*, type; incomplete dorsal shield, National Museum of Canada 10036 (× 3). A, dorsal view; B, lateral view of left side; C, rostral view.

*bro*, branchial opening; *mrp*, median rostral process; *orb*, orbit; *pop*, preorbital process; *rep*, rostral epitegum.

terminated quite abruptly anteriorly, that is, at the posterior borders of the branchial openings.

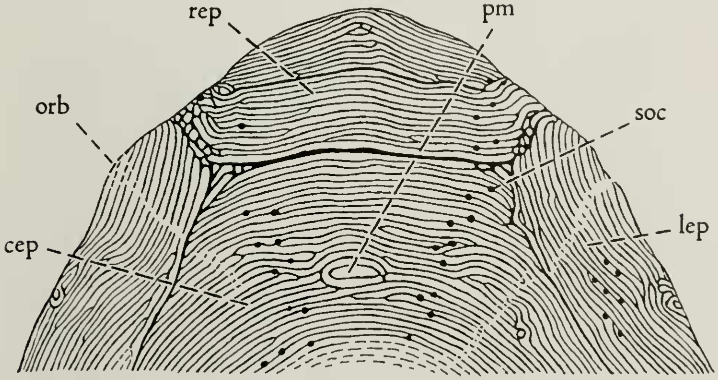

FIG. 124. *Vernonaspis sekwiae*, type; anterior part of dorsal shield, National Museum of Canada 10036 (× 5).

*cep*, central epitegum; *lep*, lateral epitegum; *orb*, orbit; *pm*, pineal macula; *rep*, rostral epitegum; *soc*, pores of supraorbital sensory canal.

**Vernonaspis sekwiae** new species. Figures 100,C, 123–124.

*Type.*—National Museum of Canada 10036, dorsal shield, complete anteriorly but preserved only as an internal impression in the posterior two-thirds (figs. 123–124).

*Referred specimens.*—CNHM, PF 3673, crushed dorsal shield; PF 3674, incomplete dorsal shield; PF 3675–3676, incomplete ventral shields; PF 3676–3678 and National Museum of Canada 10037, shield fragments.

*Occurrence.*—Late Silurian, probably Late Ludlovian, top of Mt. Sekwi, beside Keele River, Northwest Territories, Canada; 63° 28′ N; 128° 40′ W. (California Standard Company locality Z-29-61; horizon 4994′–5080′).

*Diagnosis.*—The dorsal shield has a length of about 33 mm., and 5½–6½ dentine ridges per millimeter. Its posterior edge is nearly transverse, probably with little or no median lobe. Its width ratio is about .64. The orbital and pineal ratios are greater than in other species.

*Discussion.*—This species is of about the same length as *Vernonaspis allenae* but is relatively broader. Proportionate width is usually difficult to determine reliably, but two dorsal shields (National Museum of Canada 10036 and PF 3674) are little flattened or distorted, while known specimens of *V. allenae* are narrower even though flattened. The dentine ridges are somewhat coarser in *V. sekwiae*, especially on the ventral shield, which has only 4–5 per mm. *V. sekwiae* differs from other *Vernonaspis* in the more posterior position of the orbits and pineal organ; the orbital ratio is .14 and the pineal ratio is .24, both within the range of *Archegonaspis*. However, these ratios may have been increased slightly by the fact that the median rostral process of the type has been bent up so that it projects somewhat anteriorly. On the rostral epitegum the ridges are all transverse (fig. 124, *rep*); there is no suggestion of any antero-posterior ridges and little tendency toward denticulation here, such as occurs in other *Vernonaspis*. A pineal macula (fig. 124, *pm*) is clearly indicated in the type by an oval ridge pattern, elongate laterally, but is not present in other specimens. The postrostral field is completely indistinguishable from the central epitegum, as is typical of *Vernonaspis*. In front of the pineal macula the ridges are transverse, and laterally these ridges curve backward into the somewhat elliptical central pattern. There are many minor irregularities in the central pattern of PF 3673.

The ventral shield is incompletely known. PF 3675 suggests that it was probably relatively flat anteriorly and deeply vaulted posteriorly. The ridges are somewhat coarser than on the dorsal shield and are arranged mostly longitudinally. Anteriorly they radiate toward the antero-lateral corners, and there may be an anterior band of transverse ridges.

This species resembles *Archegonaspis* in its relative broadness, in the posterior position of its orbits and pineal macula, and in its completely transverse rostral pattern. However, the presence of a strong median rostral process (fig. 123,C, *mrp*) and the fact that the postrostral field cannot be distinguished from the central epitegum, show its relationship to *Vernonaspis*.

### **Vernonaspis** sp.

CNHM, PF 863 (fig. 125) is a crushed and incomplete dorsal shield from the Late Silurian, Longwood shale, along the Erie Railroad tracks, Shin Hollow, about 1¾ miles south-southeast of Graham Station, Orange County, New York. The estimated total length is 45–50 mm. The median rostral and preorbital processes are moderately well developed, and the postbranchial lobes are weak. The dentine ridges are 5–6 per mm., flat-topped on the rostrum and over the orbits, round-crested centrally, and sharply crested along the lateral edges where they are somewhat finer. The rostral epitegum is covered with denticles and short ridges; antero-medially there are irregularly arranged denticles and short ridges; behind this is a band of short transverse ridges, then denticulations posteriorly. Some pores of the supraorbital canals are surrounded by circular ridges. This specimen shows many similarities to *Vernonaspis major* but is smaller and has weaker postbranchial lobes.

FIG. 125. *Vernonaspis* sp., anterior part of dorsal shield, CNHM, PF 863 (× 4).

Princeton 17043 is an incomplete dorsal shield in counterpart from the Late Silurian, High Falls formation, road cut on Delaware Water Gap–Millbrook road, opposite Shawnee Island, Warren County, New Jersey. The length of the dorsal shield is about 36 mm. and there are about 6 dentine ridges per millimeter. The epitega and ridge pattern are similar to other species of *Vernonaspis*. However, this specimen is somewhat larger than other species from this region, and the median rostral process is small.

### **Pionaspis**[1] new genus

*Type-species.—Pionaspis planicosta,* new species

*Diagnosis.*—This genus includes large-sized Cyathaspidinae with rather broad shields. The epitega are distinctly separated by ridge pattern and apparent sutures, but the postrostral field is not distinguished from the central epitegum. The dorsal shield lacks a median rostral process, has deep orbital notches, and has short, deep postbranchial lobes with their anterior edges abruptly truncate. The

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[1] From πιον, plump; and ασπις, shield.

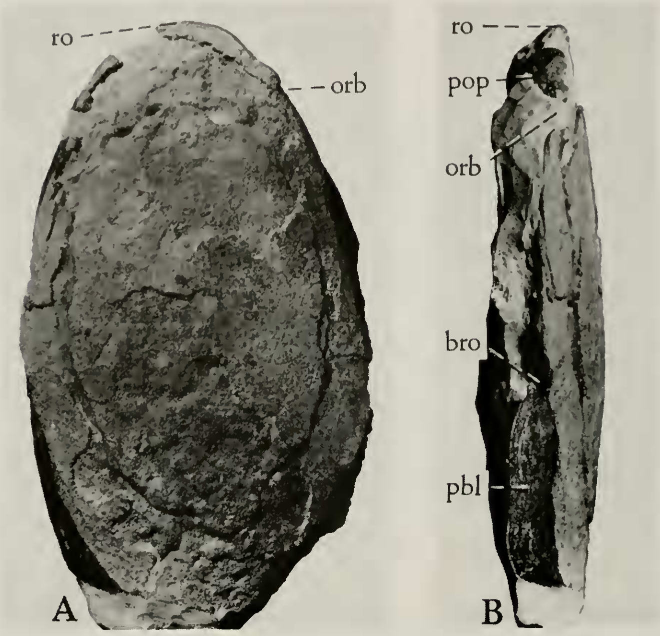

FIG. 126. *Pionaspis planicosta*, type; incomplete dorsal shield, National Museum of Canada 10035 (× 1). A, dorsal view; B, lateral view of left side.

*bro*, branchial opening; *orb*, orbit; *pbl*, postbranchial lobe; *pop*, preorbital process; *ro*, rostrum.

orbital ratio is about .14. The ridge pattern of the central epitegum, including the postrostral field, and of the ventral shield, is semi-elliptical, with the ridges converging only slightly posteriorly, but converging strongly anteriorly to form a continuous curve around the anterior end.

**Pionaspis planicosta,** new species. Figures 126–128.

*Type.*—National Museum of Canada, 10035, incomplete dorsal shield (figs. 126–127).

*Referred specimen.*—CNHM, PF 3681, ventral shield (fig. 128).

*Occurrence.*—Early Devonian, about 30 miles northwest of Muncho Lake, British Columbia, 59° 07′ 30″ N.; 126° 22′ W. (locality R5–61, 2100′ of California Standard Company).

*Diagnosis.*—The length of the dorsal shield is 77 mm., and of the ventral shield is about 65 mm. The width ratio of the dorsal shield is .62. On the dorsal shield there are 5½–6 dentine ridges per millimeter, and they are flat-topped, except that laterally and postero-

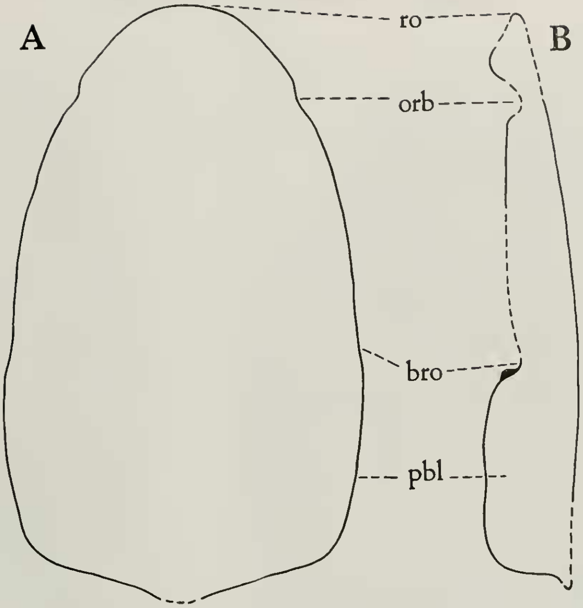

FIG. 127. *Pionaspis planicosta*, restoration of dorsal shield based on type (× 1). A, dorsal view; B, lateral view of left side.

*bro*, branchial opening; *orb*, orbit; *pbl*, postbranchial lobe; *ro*, rostrum.

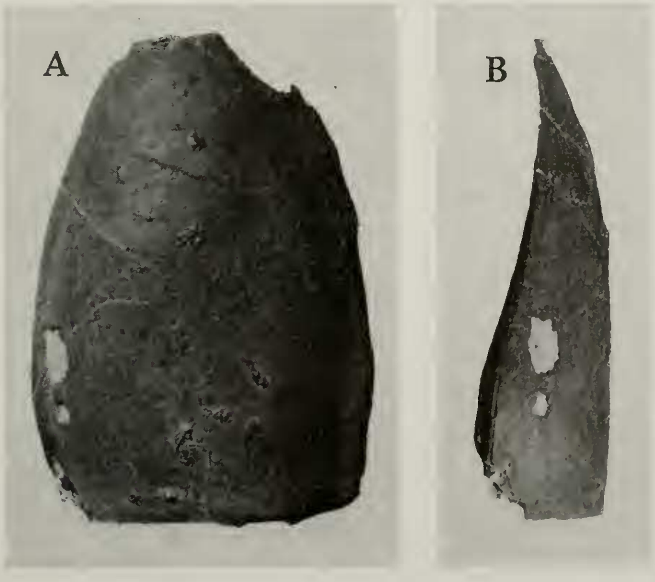

FIG. 128. *Pionaspis planicosta*, ventral shield, CNHM, PF 3681 (× 1). A, ventral view; B, lateral view of right side.

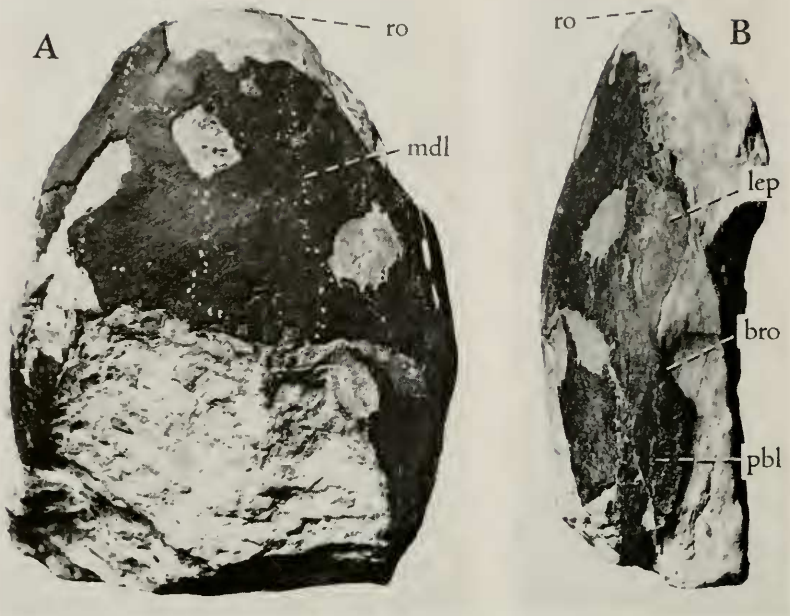

Fig. 129. *Pionaspis acuticosta*, type; incomplete dorsal shield, National Museum of Canada 10034 (×1); the pores of the lateral line canals have been marked with white ink. A, dorsal view; B, lateral view of right side.

*bro*, branchial opening; *lep*, lateral epitegum; *mdl*, medial dorsal sensory canal; *pbl*, postbranchial lobe; *ro*, rostrum.

laterally the inner edges are elevated above adjacent ridges. On the central part of the ventral shield there are 4–5 flat-topped dentine ridges per millimeter.

*Discussion.*—See *Pionaspis acuticosta.*

**Pionaspis acuticosta** new species. Figures 129–130.

*Type.*—National Museum of Canada, 10034, an incomplete dorsal shield (figs. 129–130).

*Occurrence.*—The same as *Pionaspis planicosta.*

*Diagnosis.*—The length of the dorsal shield is estimated to be about 80 mm., and the width ratio is estimated to be .75. On the dorsal shield the dentine ridges are 6½–7 per mm. centrally, and 7½–8 per mm. laterally. The ridges are sharp-crested.

*Discussion.*—With the exception of *Allocryptaspis* the two species of *Pionaspis* are the largest known cyathaspids. Their postbranchial lobes (figs. 127,B, 130,B, *pbl*) resemble those of the Irregu-

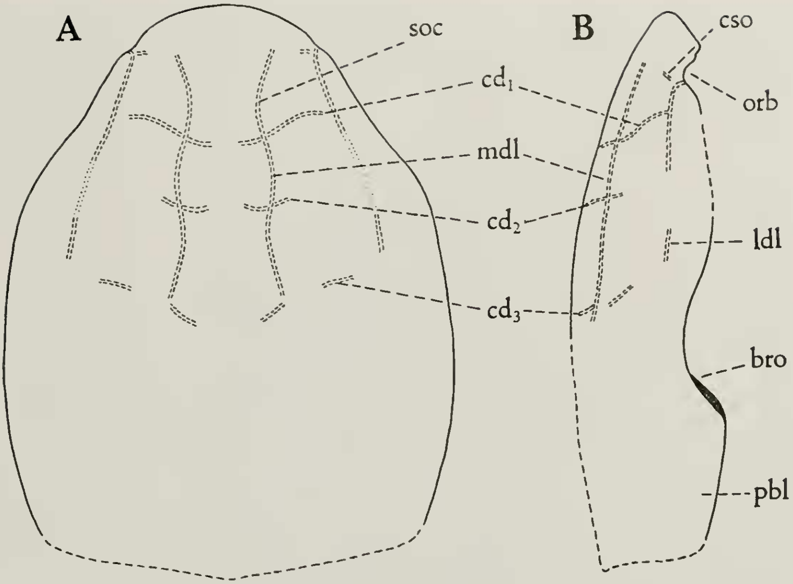

FIG. 130. *Pionaspis acuticosta*, restoration of dorsal shield based on type (× 1). A, dorsal view; B, lateral view of right side.

*bro*, branchial opening; *cd*$_{1-3}$, dorsal transverse sensory commissures; *cso*, transverse supraorbital sensory commissure; *ldl*, *mdl*, lateral and medial dorsal sensory canals; *orb*, orbit; *pbl*, postbranchial lobe; *soc*, supraorbital sensory canal.

lareaspidinae in being relatively short and deep, with the anterior edges abruptly truncate. However, *Pionaspis* apparently lacks the other characteristic features of that subfamily—the very fine dentine ridges, the much branched lateral line canals, and the posteriorly placed orbits. As far as is known, there is nothing to debar *Pionaspis* from the subfamily Cyathaspidinae.

As is commonly the case in *Vernonaspis*, two species of *Pionaspis* are found together. The length of the dorsal shields is about the same in the two species, but the breadth of the dorsal shield of *P. acuticosta* is considerably greater. The type of the latter is crushed and somewhat flattened, but this cannot account for the difference in the width ratio. A transverse measurement following the surface of the shield across the postbranchial lobes is about 75 mm. in *P. acuticosta*, but only about 60 mm. in *P. planicosta*. Moreover, the difference in shape and coarseness of the dentine ridges indicates that these are two distinct species.

The dorsal shield is only slightly arched. The median rostral process is absent, but there is a slight median convexity on the rostral margin of *P. planicosta*. The anterior border of the postbranchial lobe is turned inward to form a small process that bounds the branchial opening posteriorly (figs. 127,B, 130,B, *bro*); this process is ornamented with fine tubercles on its external part. The posterior margin of the dorsal shield of *P. planicosta* is slightly convex with a small median lobe. Little is known of the rostral epitegum. The preorbital process (fig. 126,B, *pop*), which is formed in part by the lateral part of this epitegum, is ornamented with large, flat denticles. Near the anterior margin, the rostral epitegum of *P. planicosta* is covered with transversely arranged short ridges and denticles. The lateral and central epitega are more distinct in *P. acuticosta* than in most cyathaspids; they are separated by an apparent suture, and their dentine ridges meet at an acute angle. The lateral epitegum tapers to a point and ends over the branchial notch. There are prominent irregularities in the ridge pattern of *P. acuticosta*, but these are perhaps restricted to the region along the lateral lines. The latter are indicated in *P. acuticosta* by prominent pores, each surrounded by a circular ridge. The pattern of canals (fig. 130), as far as it is determinable, is quite complete and regular.

The only ventral shield (fig. 128) is the one that has been referred to *P. planicosta* because it agrees with the latter in its type of dentine ridges. This shield was probably highly vaulted originally, but it has been somewhat crushed in preservation. Its anterior edge is approximately transverse. A small notch in one antero-lateral corner is probably for a lateral plate. The lateral edge is gently concave back to the post-branchial region, where it becomes gently convex; it has a distinct inwardly turned margin, ornamented with fine, short ridges laterally, but unornamented medially where it was presumably overlapped by the branchial plate. The posterior edge is transverse and nearly straight except for a small median lobe that has been broken off in this specimen.

### **Listraspis**[1] new genus

*Type-species.—Listraspis canadensis*, new species.

*Diagnosis.*—On the dorsal shield the lateral epitega form brims, which are ornamented on both dorsal and ventral surfaces and which extend posteriorly past the branchial openings to form projecting points at the postero-lateral corners of the shield. The branchial plates are attached to the ventro-mesial edges of the lateral brims.

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[1] From *λιστρον*, a spade; and *ασπις*, shield.

The orbits are completely surrounded by bone as a result of the fusion of the suborbital plates to the dorsal shield. The dentine ridges are very fine, with narrow crests and with lateral projections at their bases.

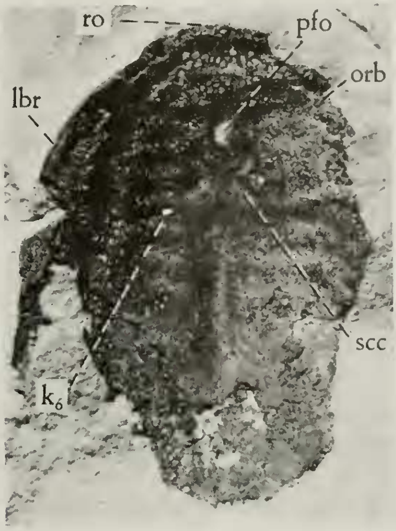

FIG. 131. *Listraspis canadensis*, type; incomplete dorsal shield exposed on inner side, National Museum of Canada 10030 (× 2).

$k_6$, fossa for sixth gill pouch; *lbr*, lateral brim; *orb*, channel leading to orbit, exposed by removal of ventral rostral lamina; *pfo*, fossa for pineal organ; *ro*, rostrum; *scc*, depressions for semicircular canals.

**Listraspis canadensis,** new species. Figures 131–133.

*Type.*—National Museum of Canada, 10030, incomplete dorsal shield exhibiting the inner side (fig. 131).

*Referred specimens.*—Incomplete dorsal shields, National Museum of Canada, 10031–10032 and CNHM, PF 3682–3685; ventral shields, National Museum of Canada, 10033, and CNHM, PF 3687–3693.

*Occurrence.*—Early Devonian, about 30 miles northwest of Muncho Lake, British Columbia, 59° 07′ 30″ N., 126° 22′ W. (locality R5–61, 2100′ of California Standard Company).

*Diagnosis.*—The length of the dorsal shield is 26–32 mm., its width ratio is usually .82–.89, its pineal ratio is .21–.24, and its orbital ratio is .13–.15. The length of the ventral shield is 24–28 mm. On the dorsal shield there are 13–14, and on the ventral shield 8–10 dentine ridges per millimeter.

*Discussion.*—This strikingly distinct cyathaspid shows some superficial resemblances to pteraspids, and at first glance appears to represent at least a distinct subfamily. The orbits (figs. 131, 133,A, *orb*) are completely encircled by the dorsal shield, but this is only the result of fusion of the usually separate suborbital plates to the shield. The postero-lateral points on the dorsal shield (fig. 133,A, *plp*) resemble the cornual plates of pteraspids, but are only extensions of the lateral epitega, not separate elements. A postero-median process on the dorsal shield (figs. 132,A, 133,A) is only a lobe of the central epitegum, not a distinct element, as is the dorsal spine of pteraspids and *Ariaspis* to which it is analogous. The fine dentine ridges are narrow-crested, and have at the base numerous projections at right angles, alternating with those of adjacent ridges; they are unlike other cyathaspid dentine ridges, and show some resemblance to the crenate ridges of pteraspids. On the dorsal shield there are well-developed lateral brims (fig. 132, *lbr*) which are ornamented with dentine ridges on both dorsal and ventral surfaces; they are roughly comparable to sharply folded branchial plates of pteraspids, though in *Listraspis* they are, of course, formed by the lateral epitega and have the branchial plates attached to their ventro-mesial edges. These resemblances of *Listraspis* to pteraspids are clearly superficial. This genus is definitely a cyathaspid, and is probably best considered as a specialized member of the subfamily Cyathaspidinae. It resembles the latter in having distinct epitega, long dentine ridges, elliptical ridge pattern on the central epitegum, and transverse pattern on the rostral epitegum.

*Listraspis canadensis* is a small cyathaspid with a broad, gently arched dorsal shield, rivaled in its width ratio only by *Ctenaspis*. One specimen (PF 3683a, fig. 133,A) is relatively narrower; its width ratio is .78, but this is a small, probably juvenile, and perhaps distorted specimen. There is also inconsistency in the width ratio as used here, for it, or more exactly the total length measurement, is influenced by the postero-median process, which is not always present.

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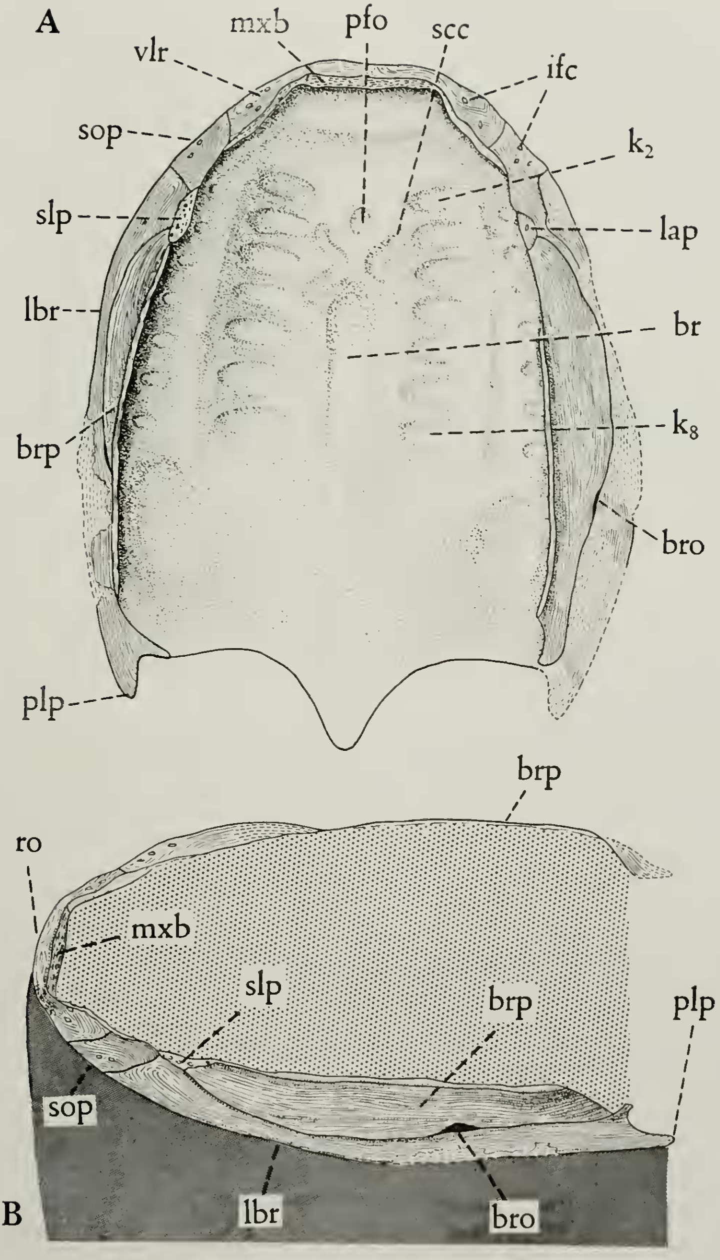
FIG. 132. *Listraspis canadensis*, dorsal shield, drawn largely from CNHM, PF 3682 (× 3). A, ventral view, with inner face restored in large part from other specimens; B, ventro-lateral view.

*br*, impression of cranial cavity; *bro*, branchial opening; *brp*, branchial plate; *ifc*, infraorbital sensory canal; $k_{2-8}$, impressions of gill pouches; *lap*, lateral plate; *lbr*, lateral brim; *mxb*, maxillary brim; *pfo*, fossa for pineal organ; *plp*, postero-lateral point; *ro*, rostrum; *scc*, impressions of semicircular canals; *slp*, sutural area for lateral plate; *sop*, suborbital plate; *vlr*, ventral lamina of rostrum.


A
mxb
pfo
scc
vlr
ifc
sop
k2
slp
lap
lbr
br
brp
k8
bro
plp
B
brp
ro
mxb
slp
brp
plp
sop
lbr
bro

The dorsal shield is clearly divisible into rostral, lateral, and central epitega. The rostral epitegum is short and has transverse dentine ridges. The anterior and lateral edges of the rostrum are turned under to form a ventral lamina (fig. 132,A, *vlr*). The postero-lateral parts of this lamina have lateral line pores (fig. 132,A, *ifc*) and are equivalent to the preorbital processes of other cyathaspids. The rest of the underturned rostral lamina is ornamented with fine ridges in short lengths, arranged parallel to the margin. The rostral margin has a slight median concavity, reflected by a corresponding convexity on the inner margin of the lamina. The maxillary brim proper (fig. 132, *mxb*) is a nearly vertical, transverse narrow face at right angles to this antero-ventral lamina, and is ornamented with fine, crenate ridges.

The central epitegum has a median, longitudinal crest in its central part. Its dentine ridges are arranged more or less elliptically (fig. 133,A), but posterior to the midpoint, the ridges meet at an angle at the midline, and anteriorly they form continuous curves through the postrostral field, which is not distinct in this genus. The pineal prominence (fig. 131, 132,A, *pfo*) is large and is only thinly covered by the shield. PF 3683a (fig. 133,A) and National Museum of Canada 10031 have a distinct postero-median process; the ridges of the central epitegum curve into it, showing that it is a part of this epitegum.

Each lateral epitegum has its ridges arranged slightly obliquely so that they meet the ridges of the central epitegum at a low angle. Anteriorly, the ridges curve up over the orbits, as is usual in cyathaspids. At the lateral margin of the shield, each lateral epitegum is folded under to form its ventral ornamented surface. The lateral margin narrows slightly but abruptly at the level of the branchial opening, and then continues posteriorly into the postero-lateral points (fig. 132, *plp*). The fact that the dentine ridges of the lateral epitegum are usually or mostly continuous into the postero-lateral point indicates that the latter is probably only a posterior extension of the lateral epitegum.

Each branchial plate attaches to the medial edge of the ventral surface of the lateral brim, and is directed ventrally or slightly medioventrally (fig. 132, *brp*). The anterior end of the branchial plate is bluntly pointed, and the posterior end, which terminates at the base of the postero-lateral point of the lateral epitegum, is obliquely truncate. The branchial opening (fig. 132, *bro*) is preserved as a slit between the branchial plate and the ventral surface of the brim formed

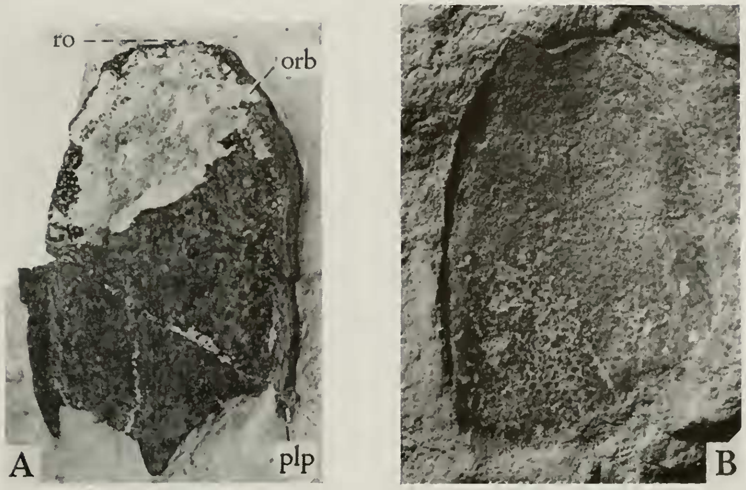


FIG. 133. *Listraspis canadensis* (× 2). A, incomplete dorsal shield, CNHM, PF 3683a; B, ventral shield, largely preserved as an impression, CNHM, PF 3687. *orb*, orbit; *plp*, postero-lateral point; *ro*, rostrum.

by the lateral epitegum, and is situated about as is usual in cyathaspids, that is, well in advance of the posterior end of the shield.

The ventral surface of the brim of the dorsal shield continues as a distinct ventral lamina anterior to the branchial plate, under the orbits, and into the much narrower ventral lamina of the rostrum. Discontinuities in the ridge pattern of PF 3682 indicate that the suborbital part of this lamina, which shows pores of the infraorbital canal, is probably a distinct plate (fig. 132, *sop*) homologous to the suborbital plate of *Anglaspis heintzi* (fig. 94,A, *sop*). The part of the ventral lamina anterior to the suborbital plate is equivalent to the preorbital process of other cyathaspids. A small plate with a single lateral line pore (fig. 132,A, *lap*), lying just in front of the anterior end of the branchial plate, is comparable to a lateral plate of pteraspids.

The internal impressions of pineal organ, brain, semicircular canals, and gill pouches are much as in other cyathaspids (fig. 132,A). There are seven pairs of gill pouches ($k_2$–$k_8$ by Stensiö's terminology), with $k_8$ lying only slightly anterior to the branchial opening.

The ventral shield (fig. 133,B) has a concave anterior border, and a strongly convex posterior border, the latter sometimes with a slight median lobe. In known specimens, this shield is only gently arched. The dentine ridge pattern is elliptical, except that the ridges flare anteriorly into a band of ridges parallel to the anterior edge.

Very little of the dorsal lateral line pattern is discernible. That of the ventral shield agrees with the typical cyathaspid condition as far as it can be made out, and has the medial transverse commissures arranged in V's.

Thin sections of both dorsal and ventral shields have been made, but because of crushing the structure of the basal and middle layers cannot be determined. The superficial layer differs from that of other cyathaspids in its narrow, widely spaced dentine ridges.

### Irregulareaspidinae

Epitega may or may not be indicated, and there is no trace of scale components on the shield. The shield is relatively broad, with the orbits and usually the pineal organ posteriorly placed. The postbranchial lobes are short, deep, and truncate anteriorly. The dentine ridges are very fine and commonly irregular. The lateral line canals are sometimes branched in a complex manner. The dermal skeleton is relatively thin. *Dikenaspis, Dinaspidella, Irregulareaspis.*

**Dikenaspis** Denison

*Type-species.—Dikenaspis yukonensis* Denison.

*Dikenaspis* Denison, 1963, Fieldiana: Geol. **14**, no. 7, pp. 116–120, 140.

*Diagnosis.*—The dorsal shield narrows anteriorly toward the orbits. The pineal organ is intermediate in position (pineal ratio=.24). The rostrum has a strong median lobe on its anterior margin (fig. 135,B, *mrp*). The dorsal shield is divided by the ridge pattern into rostral, central, and paired lateral epitega. The ridges are mostly transverse on the rostral epitegum; they converge at the midline anteriorly on the central epitegum and in the postrostral field. The lateral line canals are branched in a complex fashion; there are two pairs of lateral lines on the rostrum.

**Dikenaspis yukonensis** Denison. Figures 97,E, 101,A, 134–135.

*Dikenaspis yukonensis* Denison, 1963, Fieldiana: Geol., **14**, no. 7, pp. 117–120, figs. 66–67.

*Type.*—Princeton 17088, a nearly complete dorsal shield and the posterior part of a ventral shield (figs. 134–135).

*Occurrence.*—Probably Early Devonian (Early Downtonian) limestones and graptolitic shales,[1] Beaver River, southeastern Yukon.

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[1] Tentatively assigned to the Middle Ludlovian in Denison (1963); see (p. 450).

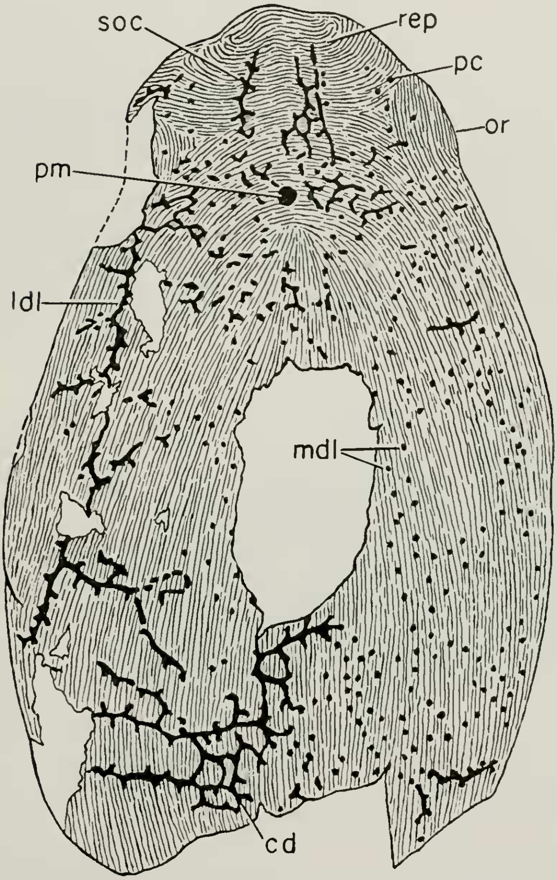

FIG. 134. *Dikenaspis yukonensis*, type (from Denison, 1963); incomplete dorsal shield, Princeton 17088 (× 4).

*cd*, branched dorsal transverse sensory commissure; *ldl*, *mdl*, lateral and medial dorsal sensory canals; *or*, orbit; *pc*, pores of ?profundus sensory canal; *pm*, position of pineal organ; *rep*, rostral epitegum; *soc*, ?supraorbital sensory canal.

*Diagnosis.*—The length of the dorsal shield is about 30 mm.; its proportions are moderately broad, with a width ratio of .63. There are 9–10 dentine ridges per millimeter.

*Discussion.*—The relationship of *Dikenaspis* to the Irregulareaspidinae is indicated by a number of characters, especially the posterior position of the orbits (orbital ratio=.17), the short, deep postbranchial lobes with abrupt anterior truncations (fig. 135, *pbl*), the complexly branched lateral lines (figs. 97,E, 134), the fine dentine ridges, and the thinness of the shield (fig. 101,A). But *Diken-*

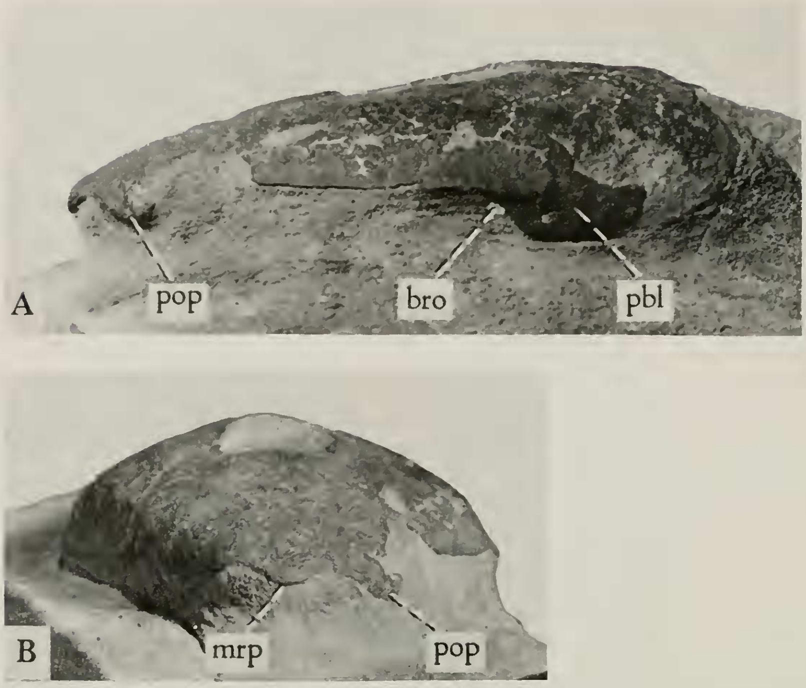

FIG. 135. *Dikenaspis yukonensis*, type; incomplete dorsal shield, Princeton 17088 (× 3). A, lateral view of left side; B, rostral view.

*bro*, branchial opening; *mrp*, median rostral process; *pbl*, postbranchial lobe; *pop*, preorbital process.

*aspis* differs from other Irregulareaspidinae in the presence of distinct epitega, indicated especially by the more or less transverse ridges of the rostral epitegum (fig. 134, *rep*), and the semi-elliptical arrangement of the anterior ridges of the combined central epitegum and postrostral field (fig. 134). An unusual feature of the lateral line system, unknown in other Cyathaspididae, is the presence of two pairs of longitudinal sensory canals on the rostrum. It is conceivable that this is a result of the excessive branching of the sensory canals. However, it may be of more fundamental significance. Some pteraspids have, in addition to the supraorbital canals, a pair of small branches directly over the orbits (e.g., *Protopteraspis primaeva*, Kiaer, 1928, fig. 1). *Traquairaspis pococki* (White, 1946, fig. 40) also has two pairs of anterior sensory canals. Holmgren (1942, p. 12) has suggested that the canals immediately over the orbits may have been innervated by the profundus nerves, and if this is so, the more medial pairs (figs. 97,E, 134, *soc*) would be homologous to the supraorbital canals of other fishes.

A ventral shield (Princeton 17377) referred here has a length of 26 mm., a width ratio of .67, and fine dentine ridges (8 or more per mm.). The anterior border is concave, the posterior border is convex with a rounded median point, and the lateral borders lack the deep incisions for branchial plates that occur in *Dinaspidella* and *Irregulareaspis*. The shield is deeply arched posteriorly but nearly flat anteriorly. The dentine ridges are longitudinally arranged posteriorly, but converge toward the midline anteriorly. The most anterior and lateral ridges are, except for irregularities, continuous around the anterior and lateral parts of the shield.

### **Dinaspidella** Strand

*Type-species.—Dinaspis robusta* Kiaer.

*Dinaspis* Kiaer (not of Leonardi 1911), 1932, Skr. Svalbard Ishavet, **52**, p. 18; White, 1935, Phil. Trans. Roy. Soc. London, (B), **225**, p. 437; Säve-Söderbergh, 1941, Zool. Bidr. Uppsala, **20**, p. 530; Føyn and Heintz, 1943, Skr. Norges Svalbard Ishavs-Undersøk., **85**, p. 43.

*Dinaspidella* Strand, 1934, Folia Zool. Hydrobiol., **5**, p. 327 (new name for *Dinaspis* Kiaer); White and Moy-Thomas, 1940, Ann. Mag. Nat. Hist., (11), **6**, p. 99; Flower and Wayland-Smith, 1952, Bull. Mus. Comp. Zool., **107**, pp. 363, 368; Denison, 1953, Fieldiana: Geol., **11**, no. 7, pp. 292, 296; 1963, Fieldiana: Geol., **14**, no. 7, pp. 117, 120; Stensiö, 1958, Traité de Zool., **13**, fasc. 1, pp. 314–317, 404.

*Diagnosis.*—The dorsal shield is of rather uniform breadth. The pineal macula is situated posteriorly (pineal ratio=.30). The dorsal shield lacks a median rostral lobe and has a very small median lobe on its posterior edge. No epitega are apparent. The rostral region has transverse ridges anteriorly and irregular whorls posteriorly; the rest of the dorsal ridge pattern is mainly longitudinal, but with irregularities. The sides of the ventral shield are deeply incised for the branchial plates. The lateral line pattern (fig. 97,C) is much as in *Poraspis* except for a transverse commissure in front of the pineal macula, a tendency toward side branches, and minor irregularities.

*Discussion.*—The name *Dinaspis* is preoccupied, and *Dinaspidella* is not available nomenclatorially because both specific names are nomina nuda.

**Dinaspidella robusta** (figs. 97,C, 136) and **D. parvula** from the Early Devonian (Gedinnian), Fraenkelryggen division, Red Bay series, Spitsbergen, were merely listed by Kiaer (1932, p. 18) as new

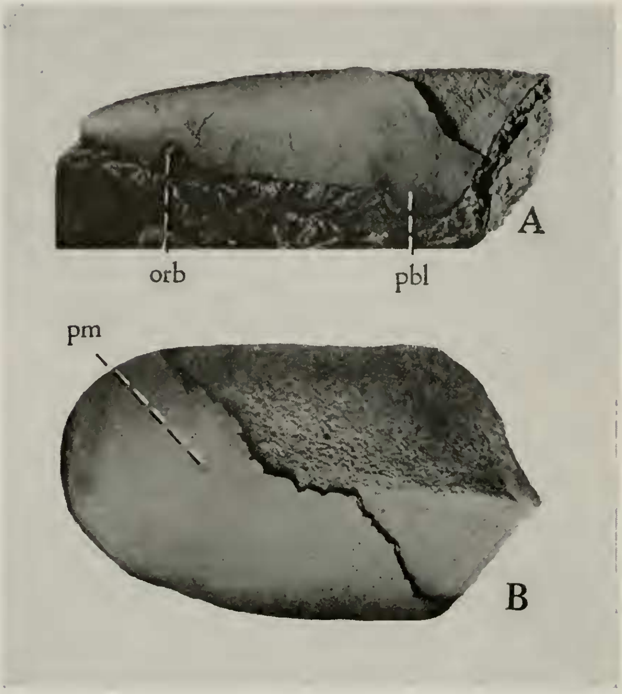

FIG. 136. *Dinaspidella robusta*, type (from Kiaer, 1932); incomplete dorsal shield, Paleontologisk Museum, Oslo, D 454 (× about 2). A, lateral view of left side; B, dorsal view.

*orb*, orbit; *pbl*, postbranchial lobe; *pm*, pineal macula.

species of *Dinaspis*. A dorsal shield (fig. 136) in the Paleontologisk Museum, Oslo, D 454 (op. cit., pl. 4, figs. 2–3) was designated as type of *D. robusta*.

### cf. **Dinaspidella** sp.

*Referred specimen.*—CNHM, PF 3871, broken and incomplete dorsal and ventral shields, associated.

*Occurrence.*—Probably Early Devonian, approximately 70 feet above top of "Ronning" dolomite, immediately west of Snake River, northern Yukon; 65° 22′ N., 133° 30′ W.; (locality Z Fx 36A of California Standard Company).

*Description and discussion.*—In the absence of sufficient diagnostic characters, the reference of this specimen to *Dinaspidella* is uncertain. The dorsal shield does not have distinct epitega. Its length and proportions are not measurable, but the orbits and indistinct pineal macula probably have a relatively posterior position. The postbranchial lobes are not preserved. The canals of the lateral line system cannot be seen, but its pores are relatively large and distinct on the dorsal shield. The orbits are well marked. The dentine ridges are very fine, 11 to 12 per mm. dorsally, and as many as 13 per mm. ventrally. The ridge pattern is largely longitudinal, but has whorls and irregularities in the anterior part of the dorsal shield, and shows a flaring towards the antero-lateral corners of the ventral shield. The ventral shield has concave lateral margins similar to those described in *Dinaspidella* and *Irregulareaspis* by Kiaer (1932). On a broken edge of the dorsal shield the chambers of the cancellous layer appear irregular, but it cannot be determined whether they have been crushed.

The specimen is associated with *Corvaspis,* and with undetermined cyathaspids. These Heterostraci occur about 40 to 50 feet above a limestone containing brachiopods and corals, which are probably of Late Silurian age according to Alfred Lenz (in litt., Dec. 20, 1963).

### **Irregulareaspis** Zych

*Type-species.—Irregulareaspis stensioi* Zych.

*Irregulareaspis* Zych, 1931, Fauna Ryb Dewonu i Downtonu Podola, pp. 83–84; White and Moy-Thomas, 1940, Ann. Mag. Nat. Hist., (11), **6**, p. 99; Denison, 1953, Fieldiana: Geol., **11**, no. 7, p. 292; 1963, Fieldiana: Geol., **14**, no. 7, pp. 117, 120.

*Irregularaspis* (in error) Kiaer and Heintz, 1935, Skr. Svalbard Ishavet, **40**, p. 82; Flower and Wayland-Smith, 1952, Bull. Mus. Comp. Zool., **107**, p. 363.

*Irregulariaspis* (in error) Stensiö, 1958, Traité de Zool., **13**, fasc. 1, pp. 296, 312, 317–318, 404.

*Dictyaspis* Kiaer (not of Haeckel, 1887), 1932, Skr. Svalbard Ishavet, **52**, p. 18; White, 1935, Phil. Trans. Roy. Soc. London, (B), **225**, p. 437.

*Dictyaspis* (*Irregularaspis*) Føyn and Heintz, 1943, Skr. Norges Svalbard Ishavs-Undersøk., **85**, p. 44; Friend, 1961, Proc. Yorkshire Geol. Soc., **33**, pt. 1, no. 5, p. 112.

*Dictyaspidella* Strand, 1934, Folia Zool. Hydrobiol., **5**, p. 327 (new name for *Dictyaspis* Kiaer); Fowler, 1947, Not. Nat. no. **187**, p. 4.

*Dictyonaspis* (in error) Berg, 1940, Trav. Inst. Zool., Acad. Sci. USSR, **5**, livr. 2, p. 110.

*Diagnosis.*—The dorsal shield is of rather uniform breadth. The indistinct pineal macula is situated posteriorly (pineal ratio=.27–.30). The posterior edges of both dorsal and ventral shields are sharply pointed medially. Epitega are probably not indicated. The dentine ridge pattern is very irregular, composed largely of whorls, and with transverse ridges only along the rostral margin. The ventral shield has deep lateral incisions for the branchial plates. The lateral line canals (figs. 97,F, 99,E) are much branched, irregular, and form a network over the shield; their pores are numerous. The dorso-lateral and ventro-lateral scales are subequal.

**Irregulareaspis stensioi** Zych

*Irregulareaspis stensiö'i* Zych, 1931, Fauna Ryb Dewonu i Downtonu Podola, pp. 83–84, drawings 46–47, photograph 5.

*Irregulaspis stensioi* Brotzen, 1936, Ark. Zool., **28A**, no. 22, p. 6.

*Type.*—Not designated.

*Occurrence.*—Early Devonian (Gedinnian), Passage Beds at top of Czortków stage, Podolia.

*Diagnosis* (based on Zych's figures).—The width ratio=.65. The pineal ratio=.27. The orbital ratio=.21. There are about 10 dentine ridges per millimeter.

**Irregulareaspis complicata** (fig. 97,F), **I. hoeli** (fig. 99,E), and **I. prisca,** from the Early Devonian (Gedinnian), Ben Nevis division, Red Bay series, Spitsbergen, were listed by Kiaer (1932, p. 19, figs. 9–10, pl. 5, pl. 6, figs. 2–3) as new species of *Dictyaspis.* They are nomina nuda. *I. hoeli* is known from a nearly complete, articulated specimen (Paleontologisk Museum, Oslo, D 474; op. cit., pl. 5).

**Irregulareaspis** sp.

*Irregulariaspis* sp. Stensiö, 1958, Traité de Zool., **13**, fasc. 1, fig. 175.

*Occurrence.*—Early Devonian (listed as "Downtonien," but presumably from the Czortków stage, Dittonian), Podolia.

### Poraspidinae

Epitega are indicated faintly or not at all and no scale components are evident. The dentine ridges are long and the ridge pattern is mostly longitudinal, although it is commonly radiating on the anterior parts of the dorsal and ventral shields, and diagonal on the lateral parts of the dorsal shield. *Poraspis, Americaspis, Homalaspidella, Ariaspis, Anglaspis, Allocryptaspis.*

**Poraspis** Kiaer

*Type-species.—Holaspis sericeus* Lankester.

*Holaspis* Lankester (not of Gray, 1863) 1873, Geol. Mag., **10**, pp. 242–243; Claypole, 1892, Quart. Jour. Geol. Soc., London, **48**, pp. 546, 551.

*Cyathaspis* (in part) von Alth, 1874, Abh. Geol. Reichanst., Wien, **7**, p. 46; Leriche, 1906, Mém. Soc. Géol. Nord, **5**, pp. 22–25.

*Palaeaspis* (in part) Woodward, 1891, Cat. Fossil Fishes Brit. Mus. (Nat. Hist.), **2**, p. 169; Stensiö, 1926, Ark. Zool., **18A**, no. 19, pp. 2–3, 12; Zych, 1931, Fauna Ryb Dewonu i Downtonu Podola, p. 84; Brotzen, 1933, Palaeobiol., **5**, pp. 431–432; White, 1935, Phil. Trans. Roy. Soc. London, (B), **225**, p. 437.

*Poraspis* Kiaer, 1930, Skr. Svalbard Ishavet, **33**, p. 4 (new name for *Holaspis* Lankester); 1932, Skr. Svalbard Ishavet, **52**, pp. 13–14; Kiaer and Heintz, 1935, Skr. Svalbard Ishavet, **40**, pp. 51–59; Heintz, 1938, Naturwiss., **28**, pp. 50–51; Säve-Söderbergh, 1941, Zool. Bidr. Uppsala, **20**, p. 534; Holmgren, 1942, K. Svensk. Vetensk.-Akad. Handl., (3), **20**, no. 1, p. 12; Wängsjö, 1952, Skr. Norsk Polarinst., **97**, p. 562; Flower and Wayland-Smith, 1952, Bull. Mus. Comp. Zool., **107**, pp. 360–361; Denison, 1953, Fieldiana: Geol., **11**, no. 7, pp. 293, 296, 303–304; 1960, Fieldiana: Geol., **11**, no. 10, pp. 556, 558, 559, 567; Stensiö, 1958, Traité de Zool., **13**, fasc. 1, pp. 296, 314–318, 352–353, 366, 384, 386, 391, 393, 404.

*Diagnosis.*—The rostral region narrows somewhat in front of the orbits, and its anterior border has a slight median convexity. The maxillary brim is broad and is covered with ridges parallel to the anterior edge. The postbranchial lobes of the dorsal shield are long and strongly developed. The posterior edges of the dorsal and ventral shields have pronounced, rounded, median lobes. The dentine ridges are fine, 7–8 per mm. Epitega are faintly or not at all indicated. The dentine ridge pattern is mostly longitudinal, except that it is sometimes fanned or irregular on the rostrum and on the anterior triangle of the ventral shield, and there are generally one or more ridges parallel to the anterior edges of the shields. The pineal macula is distinct. The lateral line pores and canals are large.

*Discussion.—Poraspis* is most closely related to *Homalaspidella* and *Americaspis*. It is the only genus of cyathaspids that is well enough known so that the course of its evolutionary changes may be determined. In the Spitsbergen species, which range throughout the Red Bay series, the following evolutionary trends are indicated (Kiaer and Heintz, 1935, pp. 125–126): (1) the size increases; (2) the dentine ridge pattern becomes more longitudinal; (3) the lateral line canals tend to form a more completely united network, and most particularly, the posterior ends of the supraorbital canals unite with the medial dorsal canals. Among the Spitsbergen and western European species two groups may be distinguished; the Podolian species are grouped separately because they are inadequately known.

Group A: Small, primitive species with the dorsal shield less than 40 mm. long, with the orbits anterior (orbital ratio=.14–.16), and with the shields rather broad (width ratio usually more than .50).

**Poraspis subtilis** Kiaer and Heintz

*Poraspis subtilis* Kiaer, 1932, Skr. Svalbard Ishavet, **52**, p. 14 (nomen nudum); Kiaer and Heintz, 1935, Skr. Svalbard Ishavet, **40**, pp. 81–82, fig. 23, pl. 21, fig. 1, pl. 22.

*Type.*—Paleontologisk Museum, Oslo, D 1904, dorsal shield.

*Occurrence.*—Early Devonian (Gedinnian), Plant horizon, Fraenkelryggen division, Red Bay series, Spitsbergen.

*Diagnosis.*—A small species (length dorsal shield=26 mm.) with a rather narrow shield (width ratio=.52) and with the orbits rather posterior (orbital ratio=.16). The dorsal shield narrows rather evenly in front of mid-length, and the dentine ridges on the rostrum are fanned.

*Discussion.*—This is the earliest known species of *Poraspis*. The narrow proportions and the rather posterior orbits suggest that it may be ancestral to the species of Group B.

**Poraspis brevis** Kiaer and Heintz

*Poraspis brevis* Kiaer, 1932, Skr. Svalbard Ishavet, **52**, p. 14, pl. 2 (nomen nudum); Kiaer and Heintz, 1935, Skr. Svalbard Ishavet, **40**, pp. 78–79, figs. 20–22, pls. 14–15.

*Type.*—Paleontologisk Museum, Oslo, D 304, dorsal shield.

*Occurrence.*—Early Devonian (Gedinnian), Primaeva and Polaris horizons, Fraenkelryggen division Red Bay series, Spitsbergen.

*Diagnosis.*—A small species (length dorsal shield=25–28 mm.) with a broad shield (width ratio=.56–.66) and anterior orbits (orbital ratio=.14).

*Discussion.*—*P. brevis* differs from *P. polaris* only in its smaller size.

**Poraspis polaris** Kiaer. Figures 98,A, 99,A, 102,A, 137.

*Poraspis polaris* Kiaer, 1930, Skr. Svalbard Ishavet, **33**, fig. 3*a–b;* 1932, Skr. Svalbard Ishavet, **52**, p. 14, figs. 1–2, pl. 1; Kiaer and Heintz, 1935, Skr. Svalbard Ishavet, **40**, pp. 59–78, figs, 2, 3, 5, 7–14, pls. 1–8, pl. 9, fig. 2, pl. 10, fig. 1, pls. 11–13, pl. 26, fig. 1, pl. 31, fig. 1, pl. 32, fig. 2, pl. 34, figs. 1–5, pls. 35–37, pl. 38, fig. 1; Säve-Söderbergh, 1941, Zool. Bidr. Up-

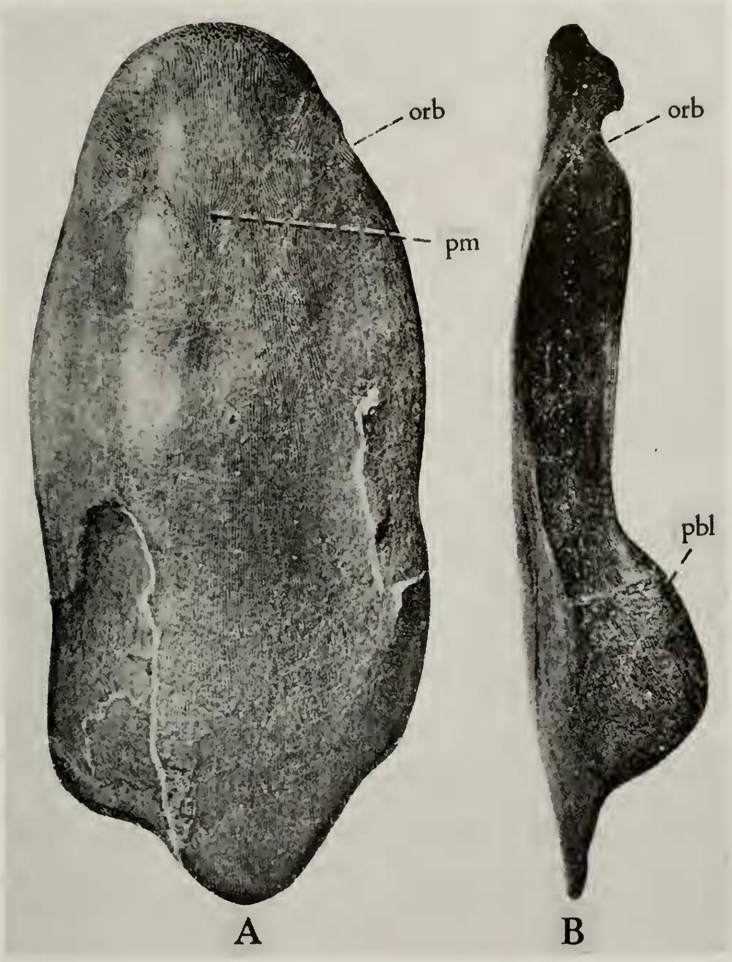

FIG. 137. *Poraspis polaris*, type (from Kiaer and Heintz, 1935); dorsal shield, Paleontologisk Museum, Oslo, D 665 (× 3). A, dorsal view; B, lateral view of right side.

*orb*, orbit; *pbl*, postbranchial lobe; *pm*, pineal macula.

psala, **20**, fig. 5; Holmgren, 1942, K. Svensk. Vetensk.-Akad. Handl., (3), **20**, no. 1, p. 10, fig. 7.

*Type.*—Paleontologisk Museum, Oslo, D 665, dorsal shield (fig. 137).

*Occurrence.*—Early Devonian (Gedinnian), Primaeva, Polaris, and Anglaspis horizons, Fraenkelryggen division, Red Bay series, Spitsbergen.

*Diagnosis.*—The length of the dorsal shield=30–40 mm., width ratio=.45–.65. The orbital ratio=.15–.16. The rostrum is faintly constricted anterior to the orbits. The rostral ridge pattern is usually longitudinal but is often fanned in earlier forms. The postbranchial part is long.

*Discussion.*—Kiaer and Heintz (loc. cit.) distinguished a *forma angusta* and a *forma lata* of *P. polaris,* and considered that the great difference in the width ratio might be a secondary sexual character. It is suggested below (p. 415) that many of these proportional differences may be the result of distortion.

### **Poraspis intermedia** Kiaer and Heintz

*Poraspis intermedia* Kiaer, 1932, Skr. Svalbard Ishavet, **52**, p. 14 (nomen nudum); Kiaer and Heintz, 1935, Skr. Svalbard Ishavet, **40**, pp. 79–81 pls. 16–17.

*Type.*—Paleontologisk Museum, Oslo, D 1308, dorsal shield.

*Occurrence.*—Early Devonian (Gedinnian), Anglaspis horizon, Fraenkelryggen division, Red Bay series, Spitsbergen.

*Diagnosis.*—The length of the dorsal shield=26–28 mm., and its width ratio=.53–.65. The orbits are anterior (orbital ratio=.14) and the rostrum is not constricted anterior to the orbits. The postbranchial region is short.

Group B: Larger species (dorsal shields longer than 36 mm.) with more slender shields (width ratio=.50 or less), and with the orbits farther back (orbital ratio=.16–.20). The supraorbital canals tend to unite with the medial dorsal canals.

### **Poraspis elongata** Kiaer and Heintz

*Poraspis elongata* Kiaer, 1932, Skr. Svalbard Ishavet, **52**, p. 14 (nomen nudum); Kiaer and Heintz, 1935, Skr. Svalbard Ishavet, **40**, pp. 82–84, figs. 24–26, pl. 9, fig. 3, pl. 10, fig. 2, pls. 18–20, pl. 21, fig. 2, pl. 27, fig. 1; Denison, 1953, Fieldiana: Geol., **11**, no. 7, p. 300.

*Type.*—Paleontologisk Museum, Oslo, D 141a, dorsal shield.

*Occurrence.*—Early Devonian (Gedinnian), Primaeva and Polaris horizons, Fraenkelryggen division, Red Bay series, Spitsbergen.

*Diagnosis.*—The length of the dorsal shield is 36–40 mm., and its proportions are relatively slender (width ratio=.44–.46). The orbits are posterior (orbital ratio=.18), and the postbranchial part is long. The dentine ridges are mostly longitudinal, but curve slightly anterolaterally on the rostrum.

*Discussion.*—This species approaches the larger and more elongated species of the overlying Ben Nevis division, such as *P. rostrata.*

*Poraspis* cf. *elongata* has been reported by White (*in* Clarke, B. B., 1951, Trans. Woolhope Nat. Field Club, **33**, pp. 236–237, fig. 9) from the Early Dittonian (zone of *Protopteraspis leathensis*), Dinmore Hill, Herefordshire, England.

**Poraspis rostrata** Kiaer and Heintz

*Poraspis rostrata* Kiaer, 1932, Skr. Svalbard Ishavet, **52**, p. 14, pl. 3, figs. 1–2 (nomen nudum); Kiaer and Heintz, 1935, Skr. Svalbard Ishavet, **40**, pp. 85–88, figs. 27–28, pls. 23–25, 39; Holmgren, 1942, K. Svensk. Vetensk.-Akad. Handl., (3), **20**, no. 1, pp. 9, 10.

*Type.*—Paleontologisk Museum, Oslo, D 124, dorsal shield.

*Occurrence.*—Early Devonian (Gedinnian), lower part of Ben Nevis division, Red Bay series, Spitsbergen.

*Diagnosis.*—A relatively large species (length of dorsal shield=45–51 mm.) with a narrow shield (width ratio=.44–.45), posterior orbits (orbital ratio=.20), and a long postbranchial part. The dentine ridges are fanned on the rostrum. The medial dorsal canals coalesce with the supraorbital canals, and the latter nearly meet in the midline.

**Poraspis barroisi** (Leriche)

*Cyathaspis barroisi* Leriche, 1906, Ann. Soc. Géol. Nord, **35**, pp. 339–340, figs. 1–2; 1906, Mém. Soc. Géol. Nord, **5**, pp. 18, 19, 21, 25–26, figs. 6–7, pl. 1, figs. 1–5.

*Pteraspis barroisi* Zych, 1927, Sérv. Géol. Pologne, Trav., **2**, livr. 1, p. 52.

*Poraspis barroisi* Kiaer, 1930, Skr. Svalbard Ishavet, **33**, p. 4; 1932, Skr. Svalbard Ishavet, **52**, p. 14; Kiaer and Heintz, 1935, Skr. Svalbard Ishavet, **40**, pp. 101–104, figs. 36–37.

*Lectotype.*—Selected by Kiaer and Heintz (1935); internal mold of dorsal shield in collections of Université de Lille, figured by Leriche (1906, pl. 1, fig. 2).

*Occurrence.*—Early Devonian (upper part of Early Gedinnian), Psammites de Liévin, Pas de Calais, France.

*Diagnosis.*—The dorsal shield has a length of 42–44 mm., and a width ratio of about .50. The orbital ratio is .17–.18. The rostral ridges are mostly longitudinal, but irregular anteriorly.

**Poraspis cylindrica** Kiaer and Heintz. Figure 106.

*Poraspis cylindrica* Kiaer, 1932, Skr. Svalbard Ishavet, **52**, p. 14, pl. 3, fig. 3 (nomen nudum); Kiaer and Heintz, 1935, Skr. Svalbard Ishavet, **40**, pp.

88–92, figs. 29–30, pl. 26, fig. 2, pl. 27, fig. 2, pl. 29, fig. 1; Stensiö, 1958, Traité de Zool., **13**, fasc. 1, fig. 179B.

*Type.*—Paleontologisk Museum, Oslo, D 205, dorsal shield, mostly an internal impression (fig. 106).

*Occurrence.*—Early Devonian (Gedinnian), upper part of Ben Nevis division, Red Bay series, Spitsbergen.

*Diagnosis.*—The dorsal shield has a length of 46–53 mm. and a width ratio of .43–.50. It is slightly constricted at the orbits and the orbital ratio is .17. The rostral ridges are fanned. The medial dorsal canals meet the supraorbital canals, but the transverse commissures do not meet the lateral dorsal canals.

*Discussion.*—This species is similar to *P. rostrata* and *P. barroisi.*

### **Poraspis magna** Kiaer and Heintz

*Poraspis magna* Kiaer, 1932, Skr. Svalbard Ishavet, **52**, p. 14. (nomen nudum); Kiaer and Heintz, 1935, Skr. Svalbard Ishavet, **40**, pp. 92–97, figs. 31–32, pls. 28, 29, figs. 2, 4, pl. 38, fig. 2; Säve-Söderbergh, 1941, Zool. Bidr. Uppsala, **20**, fig. 4.

*Type.*—Paleontologisk Museum, Oslo, D 203, dorsal shield.

*Occurrence.*—Early Devonian (Gedinnian), upper part of Ben Nevis division, Red Bay series, Spitsbergen.

*Diagnosis.*—The length of the dorsal shield is 52–62 mm. and the width ratio is .44–.50. The orbital ratio is .18, and there is no abrupt constriction at the orbits. The dentine ridge pattern is longitudinal except for a slight fanning on the rostrum. The lateral line pattern is similar to that of *P. cylindrica.*

*Discussion.*—This species may have been derived from *P. cylindrica,* from which it differs in its larger size.

### **Poraspis sericea** (Lankester)

*Holaspis sericeus* Lankester, 1873, Geol. Mag., **10**, pp. 241, 331–332, pl. 10.

*Palaeaspis sericea* Woodward, 1891, Cat. Fossil Fishes Brit. Mus. (Nat. Hist.), **2**, p. 169; Stensiö, 1926, Ark. Zool., **18A**, no. 19, pp. 1, 7, fig. 6.

*Palaeaspis* (*Poraspis*) *sericea* Zych, 1931, Fauna Ryb Dewonu i Downtonu Podola, fig. 18.

*Poraspis sericea* Kiaer, 1930, Skr. Svalbard Ishavet, **33**, p. 4; 1932, Skr. Svalbard Ishavet, **52**, pp. 13, 14; Kiaer and Heintz, 1935, Skr. Svalbard Ishavet, **40**, pp. 98–101, figs. 6, 33–35; Holmgren, 1942, K. Svensk. Vetensk.-Akad. Handl., (3), **20**, no. 1, pp. 9, 10; White, 1950, Bull. Brit. Mus. (Nat. Hist.), Geol., **1**, p. 56; Bystrow, 1955, Akad. Nauk SSSR., Mem. Vol. A. S. Berg, pp. 488–491, figs. 16–18; Ball and Dineley, 1961, Bull. Brit. Mus. (Nat. Hist.), Geol., **5**, p. 202.

*Poraspis* (*Palaeaspis*) *sericea* White, 1935, Trans. Woolhope Nat. Field Club, **1930–1932**, pt. 3, pp. 179–180, figs. 3–4.

*Type.*—British Museum (Natural History), P 4117, dorsal shield.

*Occurrence.*—Early Devonian (Middle Dittonian), Monmouthshire and Herefordshire, Great Britain.

*Diagnosis.*—The length of the dorsal shield is 70–72 mm., and its width ratio is .44. The orbital ratio is .19. The lateral line system is very regular and complete, with all the branches united.

*Discussion.*—This is the largest species of *Poraspis* and may be related to *P. magna.*

Group C: The four species described from Podolia resemble Group B in being rather large and slender, but they have not been adequately characterized. *Poraspis* also occurs south of the Dniester in equivalent deposits in Bucovina and Bessarabia.

### **Poraspis simplex** (Brotzen)

*Palaeaspis simplex* Brotzen, 1933, Palaeobiol., **5**, p. 432, pl. 24, fig. 3; 1936, Ark. Zool., **28A**, no. 22, p. 6.

*Poraspis simplex* Kiaer and Heintz, 1935, Skr. Svalbard Ishavet, **40**, pp. 52, 107.

*Type.*—A dorsal shield, not designated, in Geologisch-paleontologisch Institut, Berlin.

*Occurrence.*—Early Devonian (Gedinnian), Czortków stage, Podolia.

*Diagnosis.*—The length of the dorsal shield is 50 mm., and the width ratio is .46. The dentine ridges are mostly longitudinal, irregular on the rostrum.

### **Poraspis sturi** (von Alth)

*Cyathaspis sturi* von Alth, 1874, Abh. Geol. Reichanst., Wien, **7**, p. 46, pl. 5, figs. 1–2; 1886, Beitr. Pal. Geol. Österr.-Ung., **5**, Heft 3, pp. 64, 72; Siemiradzki, 1906, Beitr. Pal. Geol. Österr.-Ung., **19**, Heft 4, p. 214.

"*Pteraspis*" (*Cyathaspis*) *sturi* Zych, 1927, Sérv. Géol. Pologne, Trav., **2**, livr. 1, p. 52, pl. 2, figs. 1–2.

*Poraspis sturi* Kiaer, 1932, Skr. Svalbard Ishavet, **52**, p. 14; Kiaer and Heintz, 1935, Skr. Svalbard Ishavet, **40**, pp. 52, 104–105, fig. 38; Stensiö, 1958, Traité de Zool., **13**, fasc. 1, pp. 386, 401.

*Palaeaspis sturi* Brotzen, 1936, Ark. Zool., **28A**, no. 22, p. 6.

*Type.*—Not designated.

*Occurrence.*—Early Devonian (Gedinnian), Czortków stage and ?Old Red, Stage I, Podolia.

*Diagnosis.*—The dorsal shield is long (length about 60 mm.) and narrow (width ratio=.39).

*Discussion.*—The specimen referred here by Zych (1927, pl. 2, fig. 1) does not belong, according to Kiaer and Heintz.

### **Poraspis siemiradzkii** (Zych)

*Palaeaspis* (*Poraspis*) *siemiradzkii* Zych, 1931, Fauna Ryb Dewonu i Downtonu Podola, drawings 37–39, photographs 3–4, 6–7; Brotzen, 1936, Ark. Zool., **28A**, no. 22, p. 6.

*Poraspis siemiradzkii* Kiaer and Heintz, 1935, Skr. Svalbard Ishavet, **40**, p. 106, fig. 39; Holmgren, 1942, K. Svensk. Vetensk.-Akad. Handl., (3), **20**, no. 1, p. 10.

*Type.*—Not designated.

*Occurrence.*—Early Devonian (Gedinnian), Passage beds of Czortków stage, Podolia.

*Diagnosis.*—The length of the dorsal shield is 56 mm., and its width ratio is .44. The orbital ratio is about .15. The rostral ridge pattern is irregular. The lateral line pattern is very completely developed.

### **Poraspis pompeckji** (Brotzen)

*Palaeaspis pompeckji* Brotzen, 1933, Palaeobiol., **5**, pp. 433–435, fig 2, pl. 24, figs. 1, 2, 4; 1936, Ark. Zool., **28A**, no. 22, p. 6.

*Poraspis pompeckji* Kiaer and Heintz, 1935, Skr. Svalbard Ishavet, **40**, pp. 52, 107, fig. 40; Holmgren, 1942, K. Svensk. Vetensk.-Akad. Handl., (3), **20**, no. 1, p. 9; Stensiö, 1958, Traité de Zool., **13**, fasc. 1, p. 386, figs. 179A, 193, 194A–C, 203A, 206, 209.

*Type.*—Not designated, in Geologisch-paleontologisch Institut, Berlin.

*Occurrence.*—Early Devonian (Gedinnian), Old Red, Stage I, Podolia.

*Diagnosis.*—The dorsal shield has a length of 54–58 mm., a width ratio of .45–.48, and is narrowed at the orbits. The orbital index is .17. The dentine ridges are longitudinal, except for fanning on the rostrum.

### **Poraspis** sp.

*Poraspis* sp. Zych, 1931, Fauna Ryb Dewonu i Downtonu Podola, photographs 8, 9, 12, 13.

*Occurrence.*—Early Devonian (Gedinnian), Czortków stage and Old Red I, Podolia.

*Poraspis* sp. White, 1950, Bull. Brit. Mus. (Nat. Hist.), Geol., **1**, pp. 56, 74–75; 1961, Bull. Brit. Mus. (Nat. Hist.), Geol., **5**, p. 246; Ball and Dineley, 1961, Bull. Brit. Mus. (Nat. Hist.), Geol., **5**, pp. 201, 202, 219, 221, 226, 229, 231, table 1.

*Occurrence.*—Early Devonian (Late Downtonian to Middle Dittonian), Shropshire, England.

**Americaspis** White and Moy-Thomas

*Type-species.*—*Palaeaspis americana* Claypole.

*Glyptaspis* Claypole, Nov. 1884, Geol. Mag., (3), **1**, p. 520 (nomen nudum).

*Palaeaspis* Claypole (not of Gray, 1870), Dec. 1884, Amer. Nat., **18**, p. 1224; 1885, Quart. Jour. Geol. Soc. London, **41**, p. 62; 1892, Quart. Jour. Geol. Soc. London, **48**, pp. 549–561; Woodward, 1891, Cat. Fossil Fishes Brit. Mus. (Nat. Hist.), **2**, p. 169; Kiaer, 1932, Skr. Svalbard Ishavet, **52**, p. 15.

*Americaspis* White and Moy-Thomas, 1941, Ann. Mag. Nat. Hist., (11), **7**, p. 397 (new name for *Palaeaspis* Claypole); Fowler, 1947, Not. Nat. no. **187**, p. 3; Flower and Wayland-Smith, 1952, Bull. Mus. Comp. Zool., **107**, pp. 361–362; Stensiö, 1958, Traité de Zool., **13**, fasc. 1, p. 312.

*Diagnosis.*—The margin of the rostrum has a small median lobe separated by concavities from the preorbital processes. The orbits are placed anteriorly (orbital ratio=.12–.14). There is no pineal macula. The postbranchial lobes of the dorsal shield are long but weakly developed. The posterior edges of the dorsal and ventral shields have small, rounded median lobes. The general pattern of the dentine ridges (fig. 140) is much as in *Poraspis,* but it is usually modified by sinuosities or irregularities. The canals and pores of the lateral line system are small; the pattern of the lateral lines (fig. 98,C) resembles that of *Poraspis,* but both the longitudinal and transverse canals are interrupted, and the commissures between the infraorbital and supraorbital canals are absent.

*Discussion.*—*Americaspis* is very similar to *Poraspis,* from which it is distinguished as follows: the median lobe on the anterior margin of the rostrum is somewhat stronger; the orbits are usually more anterior; the dorsal shield does not narrow abruptly in front of the orbits; there is no pineal macula; the posterior edges of the dorsal and ventral shields have only small median lobes; the dentine ridge pattern (fig. 140) is characteristically sinuous or irregular, and shows on the rostrum a greater tendency toward radiation or transverseness than in most species of *Poraspis;* the ridge pattern on the central epitegum is slightly elliptical; the lateral epitega, with their diagonally arranged ridges, are more distinct; the lateral line system differs as stated in the diagnosis.

**Americaspis americana** (Claypole). Figures 98,C, 138–140, 160.

*Glyptaspis elliptica* Claypole, Nov. 1884, Geol. Mag., (3) **1**, p. 520 (nomen nudum).

*Glyptaspis bitruncata* Claypole, Nov. 1884, Geol. Mag., (3) **1**, p. 520 (nomen nudum).

*Palaeaspis americana* Claypole, Dec. 1884, Amer. Nat., **18**, p. 1224 (nomen nudum); 1885, Quart. Jour. Geol. Soc. London, **41**, p. 62, fig. 7; 1892, Quart. Jour. Geol. Soc. London, **48**, pp. 549–561, figs. 1–8; Woodward, 1891, Cat. Fossil Fishes Brit. Mus. (Nat. Hist.), **2**, p. 170; Eastman, 1907, New York St. Mus., Mem., **10**, pp. 29–30; 1917, Proc. U. S. Nat. Mus., **52**, pp. 239–240; Bryant, 1926, Proc. Amer. Phil. Soc., **65**, pp. 261–264, pl. 1, fig. 1, pl. 3, fig. 1; Zych, 1931, Fauna Ryb Dewonu i Downtonu Podola, drawing 13; Kiaer, 1932, Skr. Svalbard Ishavet, **52**, p. 15.

*Palaeaspis bitruncata* Claypole, Dec. 1884, Amer. Nat., **18**, p. 1224 (nomen nudum); 1885, Quart. Jour. Geol. Soc. London, **41**, pp. 62–63, fig. 8; Bryant, 1926, Proc. Amer. Phil. Soc., **65**, pp. 264–265, fig. 1, pl. 2, fig. 3, pl. 3, figs. 2–5; Kiaer, 1932, Skr. Svalbard Ishavet, **52**, p. 15.

*Americaspis americana* Flower and Wayland-Smith, 1952, Bull. Mus. Comp. Zool., **107**, pp. 361–362; Stensiö, 1958, Traité de Zool., **13**, fasc. 1, p. 312.

*Type.*—Los Angeles County Museum $\frac{1879}{6393}$, a dorsal shield lacking the superficial layer. Flower and Wayland-Smith (1952, p. 362) concluded that Claypole's type specimens were probably destroyed in 1899 in a fire at Buchtel College, where he taught for a number of years. However, when Claypole moved from Buchtel to Throop Polytechnic Institute in Pasadena, California in 1898, apparently he took some of his collections with him. Throop Polytechnic later became the California Institute of Technology, and in 1957 its vertebrate paleontologic collections were transferred to the Los Angeles County Museum. A drawer full of "*Palaeaspis*" with a few labels, probably in Claypole's handwriting, has come to light recently in the latter institution. One of the original labels reads "counterpart of 'type,' " and specimen 6393 is quite certainly to be identified as the counterpart of the dorsal shield figured by Claypole in 1885 (fig. 7). Both part and counterpart of this specimen were figured in lateral view by Claypole in 1892 (fig. 3), when they were identified as the type. Only the counterpart is known to be preserved, and this shows none of the dentine ridges.

*Referred specimens.*—Los Angeles County Museum 6385, an incomplete dorsal shield impression, probably the one figured by Claypole in 1892 (fig. 4); 6388 and 6405, ventral shield impressions. CNHM, dorsal shields UF 938, PF 832, 837, 3269–3270, 3272, 3274, 3276–3277, 3280, 3284–3286, 3305–3307, 3309–3311; ventral shields, PF 3273, 3275, 3278–3279, 3281, 3308; dorsal and ventral shields, PF 3268, 3321–3322.

*Occurrence.*—Late Silurian, Landisburg Sandstone member of the Wills Creek formation, Landisburg, Alinda, Andersonburg, and New Bloomfield in Perry County, Pennsylvania. The type material came from the same sandstone (then called the Bloomfield Sandstone) from unknown localities in Perry County.

*Diagnosis.*—The length of the dorsal shield ranges from 50 to 68 mm. There are 5½ to 8 dentine ridges per millimeter.

*Discussion.*—When Claypole first described his two species of *Palaeaspis*, the structure of the Heterostraci was poorly known. After a controversy between Lankester, Kunth, Schmidt, von Alth, and others had concluded with the demonstration that pteraspids had ventral as well as dorsal shields, Woodward (1891, p. 170) and Claypole (1892, p. 550) decided that *Palaeaspis bitruncata* was the ventral shield of *P. americana.* This conclusion is surely correct, although Bryant (1926, p. 264) has disputed it, claiming that Claypole figured *P. bitruncata* upside down, and that it really was a dorsal shield and a valid species; neither Claypole's nor Bryant's own figures support this contention.

I have assembled a considerable number of cyathaspids from the Landisburg Sandstone at nine localities in Perry County, and with the exception of a few small shields,[1] I believe that all may be referred to *Americaspis americana.* This is in spite of the fact that the type and other remnants of Claypole's collection show very few diagnostic characters, and the precise locality from which they came is not known. The length of the type is 67 mm., while the referred dorsal shields range from 50 to 68 mm. The specimens referred to *A. americana* show great variation in their proportions; the width ratio of the type is .53, and in the referred dorsal shields it ranges from .36 to .65, so that the extremes appear to be quite distinct species. Patten (1912, fig. 244B, C) figured a broad form and a slender form from Perry County, and suggested that the difference might be sexual. Bryant (1926, p. 264) referred more slender forms to a separate species, *Palaeaspis bitruncata*, and broader forms to *P. americana.* A comparable situation occurs in the Spitsbergen Devonian from which Kiaer and Heintz (1935, pp. 53–55) described *angusta* and *lata* forms of species of *Poraspis*, and concluded that the pro-

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[1] Claypole (1892, p. 560) mentioned several small shields not over one inch long; these are also probably a distinct species.

FIG. 138. *Americaspis americana*, slab of Landisburg sandstone from near Andersonburg, Pennsylvania, with impressions of numerous shields; CNHM, PF 3321 (× 1/4).

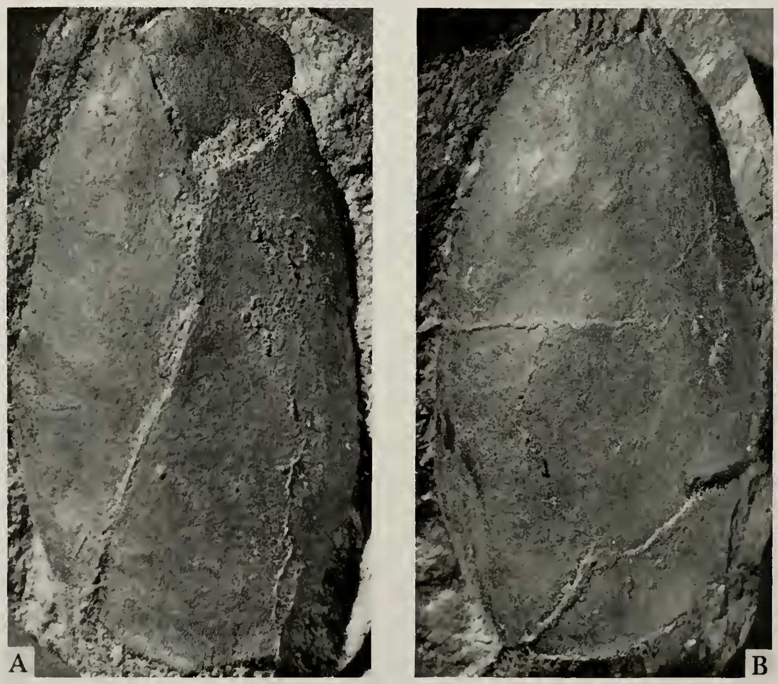

FIG. 139. *Americaspis americana* (× 3/2). A, dorsal shield, CNHM, PF 3286; B, ventral shield, CNHM, PF 3279. Both photographs are of rubber impressions of original natural molds.

portional differences were secondary sexual characters. It is possible, however, that in some of the Spitsbergen examples the proportions have been altered by distortion resulting from tectonic deformation. This is suggested by the slab figured by Kiaer and Heintz (1935, pl. 1), on which the more slender specimens are oriented in one direction, and the broader ones more or less at right angles. The same appears to be true on some slabs of *Americaspis americana* (PF 3321, fig. 138) from a locality west of Andersonburg, Pennsylvania. Measurements of Perry County specimens support the theory that the great variation in proportions is the result of deformation; the longer specimens are narrower and have finer dentine ridges, the shorter ones are broader and have coarser ridges, and all intermediates are present.

In the referred specimens, the shape (excepting proportions) and dentine ridge pattern agree with Claypole's descriptions and figures of this species. It should be noted that the "lateral plates" described by Claypole (1892, pp. 551–553, fig. 3) are the postbranchial lobes of the dorsal shield, and that the "fins" he illustrates (op. cit., pp. 553–557, figs. 6–7) are probably scales or branchial plates, as recognized by Jaekel (1894). Branchial plates were not recognized by Claypole, but are possibly represented by three imperfect specimens in his collection (Los Angeles County Museum 6386, 6402, 6409).

The pattern of the dentine ridges of *Americaspis americana* (fig. 140) is quite variable, particularly anteriorly. The postrostral field is not distinct, and the combined rostral-postrostral area shows a number of different patterns: the ridges may be fanned, curving antero-laterally and laterally toward the orbits; the pattern may be in part transverse, or it may be irregular or partly denticulate with indistinct pattern. Commonly there are two or three ridges parallel to the rostral border. On the central epitegum, the ridges, though predominantly longitudinal, usually show a slightly elliptical pattern, indicated by the angle at which the ridges of the two sides meet at the midline. There are usually prominent irregularities in the antero-lateral parts of the central epitegum. On the lateral epitega there are about four marginal ridges parallel to the edge; medial to these the ridges behind the orbits are commonly diagonal, becoming longitudinal more posteriorly. On the ventral shield (fig. 139,B) most ridges have a longitudinal or slightly elliptical pattern, commonly with a fanning toward the antero-lateral corners in the anterior triangle; the pattern in this anterior triangle is quite variable, however, and may consist of denticles or of ridges disposed in whorls.

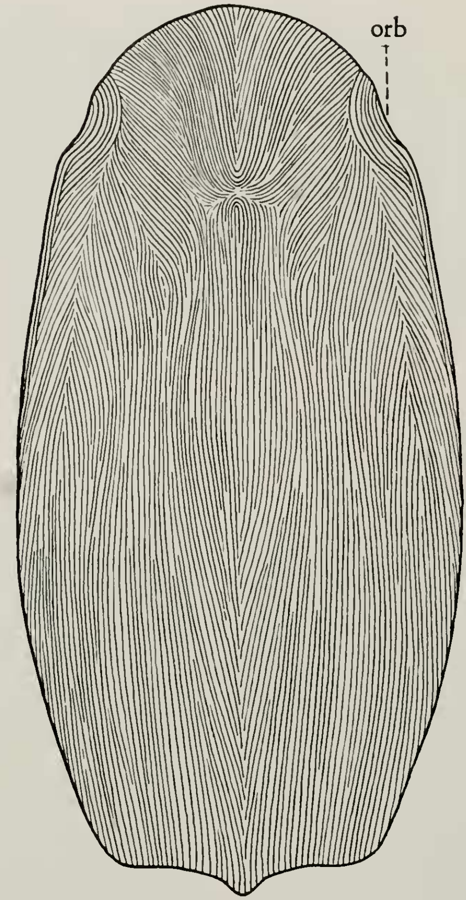

FIG. 140. *Americaspis americana*, restoration of dorsal shield in dorsal view (about × 2). Ridge pattern shown in a generalized way, with characteristic irregularities omitted; ridges actually finer than drawn.
*orb*, orbit.

The crests of the ridges are generally somewhat convex, possibly slightly flatter on the ventral shield, and higher and sharper laterally on the dorsal shield.

**Americaspis claypolei,**[1] new species. Figure 141.

*Type.*—CNHM, PF 866, an incomplete and crushed dorsal shield (fig. 141).

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[1] In honor of Edward W. Claypole (1835–1901) who described the first *Palaeaspis.*

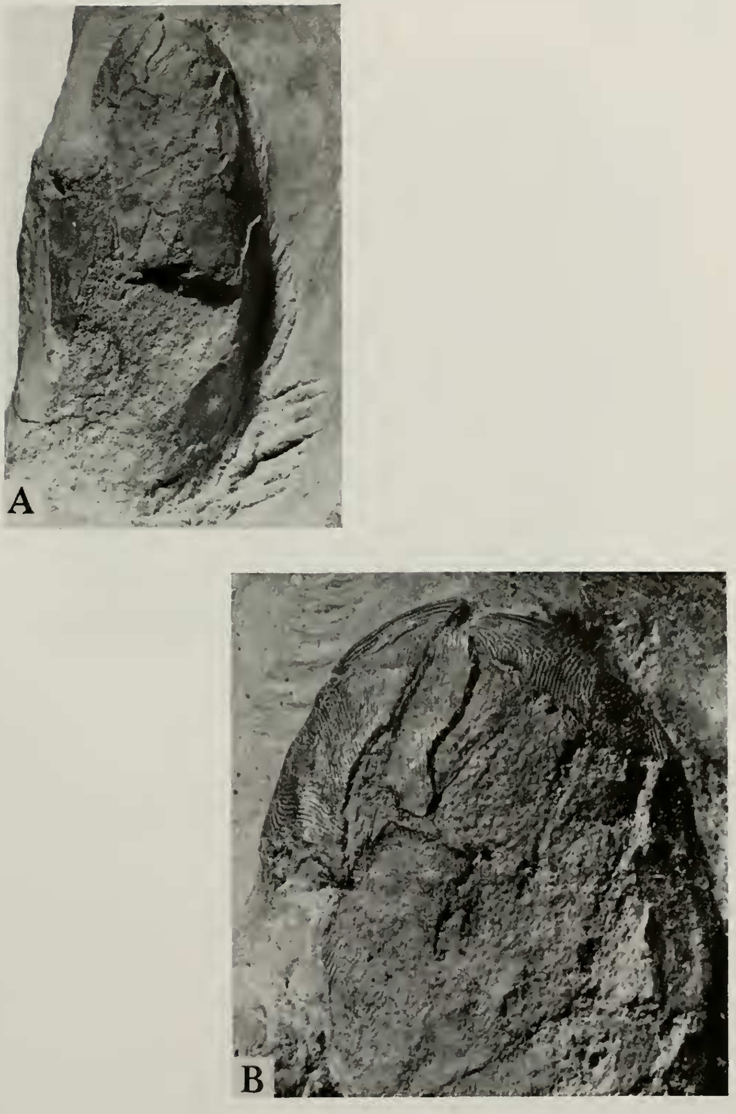

FIG. 141. *Americaspis claypolei*; A, type, incomplete and crushed dorsal shield, CNHM, PF 866, (× 4/3); B, anterior part of type, (× 4).

*Referred specimens.*—Incomplete dorsal shields, CNHM, PF 862, 3641, 3643; fragments of dorsal shields, PF 865, New York State Mus. 11469.

FIG. 142. *Americaspis* cf. *claypolei*, anterior half of dorsal shield, New York State Museum 10678 (× 3).

*Occurrence.*—Late Silurian, Longwood shale, Shin Hollow, along Erie Railroad tracks about 1¾ miles south-southeast of Graham Station, Orange County, New York.

*Diagnosis.*—The length of the dorsal shield is about 40 mm., and it is of rather narrow proportions. The dentine ridges are fine, about 6½–8 per mm., with the coarsest ones on the rostrum and over the orbits, and the narrowest ones near the lateral margins. The ridges are slightly convex centrally, sharp-crested laterally, and broad and flat-topped anteriorly on the rostrum.

*Discussion.*—The incompleteness and poor preservation of most specimens makes it difficult to characterize this species and to determine its relationships. In its known characters it agrees well with *Americaspis americana,* except in its smaller size and in its broad, flat ridges on the anterior part of the rostrum. It has a small median rostral lobe and strong preorbital processes. The postbranchial lobes are long and distinctly marked anteriorly, but are rather weakly developed. The orbits are placed anteriorly, and a pineal macula appears to be absent. The dentine ridges of the central epitegum are longitudinal or somewhat sinuous. On the lateral epitegum a few (4–7) ridges are parallel to the edge, while behind the orbits the others are diagonal anteriorly and longitudinal posteriorly. The postrostral area is probably not distinct; the ridges of the postrostral area are continuous with those of the central epitegum, and perhaps in some cases with those of the rostral epitegum. The ridge pattern of the rostral epitegum is extremely variable; usually there are 3–5 broad, flat ridges parallel to the anterior edge; behind these the ridges may be longitudinal (PF 862, 866), or denticulate anteriorly and longitudinal posteriorly (PF 865a), or all denticulate (PF 3641), or in one case mostly transverse (PF 865b).

FIG. 143. *Americaspis* sp., dorsal shield and anterior half of ventral shield, CNHM, PF 834 (× 1).

New York State Mus. 10678 (fig. 142), the anterior part of a dorsal shield from the same locality, is doubtfully referred to this species. On the rostral epitegum there are almost no ridges parallel to the anterior edge, and most of the rostral ridges radiate sinuously. This specimen has been identified as *Cyathaspis* "*wardelli*" by Flower and Wayland-Smith (1952, pl. 2, fig. 4) and by Kilfoyle (1959, p. 108).

**Americaspis** sp.

CNHM, PF 833 and 834, from the Late Silurian, Landisburg sandstone, ⅝ mile north-northwest of Landisburg, Perry County, Pennsylvania, were originally one block of sandstone containing six shields and partial shields, all similarly oriented. PF 834 (fig. 143) contains a dorsal shield and the anterior part of a ventral shield prepared to show their outer surfaces. The length of the dorsal shield is 42 mm., its width ratio is .78, and there are 5–6 dentine ridges per millimeter. It is thus smaller, broader, and coarser-ridged than *A. americana*, with which it is associated. The proportions may not be significant, but the dentine ridges differ from those of *A. americana* in being divided into short lengths, and in possessing flat crests, except for those along the lateral margins. PF 3283 from the Landisburg sandstone at Landisburg village may belong to the same species. These specimens agree with *A. claypolei* in size, but differ from it in their broader proportions and in their short, flat-crested ridges.

Three other specimens (CNHM, PF 831, 3271, and UF 937) from the Landisburg sandstone of Perry County, Pennsylvania, resemble *A. americana* except in their smaller size; the length of their dorsal shields is 42–44 mm. Their width ratio is .62–.65, and they have 6–7 dentine ridges per millimeter. They lack the broad, flat-topped anterior rostral ridges that characterize *A. claypolei.*

CNHM, PF 3282, a ventral shield from the Landisburg sandstone of Landisburg village, agrees with *A. americana* in all respects except that its dentine ridges are coarse (4½–5 per mm.) and flat-topped.

*Americaspis* appears to be present also in the Late Silurian, High Falls formation, exposed in outcrops along the Delaware Water Gap–Millbrook road, opposite Shawnee Island, Warren County, New Jersey. Three poorly preserved, obviously distorted dorsal shields (CNHM, PF 858, 860, and Princeton 18005) are referred to this genus, but are not determined specifically.

### **Homalaspidella** Strand

*Type-species.—Homalaspis nitida* Kiaer.

*Homalaspis* Kiaer (not of Reinhard 1860, nor of Milne Edwards 1863), 1932, Skr. Svalbard Ishavet, **52**, p. 14.

*Homalaspidella* Strand, 1934, Folia Zool. Hydrobiol., **5**, p. 327 (new name for *Homalaspis* Kiaer); White and Moy-Thomas, 1940, Ann. Mag. Nat. Hist., (11), **6**, p. 101; Strand, 1942, Folia Zool. Hydrobiol., **11**, p. 384; Flower and Wayland-Smith, 1952, Bull. Mus. Comp. Zool., **107**, p. 361; Stensiö, 1958, Traité de Zool., **13**, fasc. 1, pp. 314–318, 353, 369, 386, 404; Denison, 1963, Fieldiana: Geol., **14**, no. 7, pp. 123, 140.

*Homaspis* Kiaer and Heintz (not of Foerste 1868, nor of Skuse 1888), 1935, Skr. Svalbard Ishavet, **40**, pp. 127–128 (new name for *Homalaspis* Kiaer); Säve-Söderbergh, 1941, Zool. Bidr. Uppsala, **20**, pp. 533–534.

*Homolaspis* (error) White, 1935, Phil. Trans. Roy. Soc. London, (B), **225**, p. 437; Holmgren, 1942, K. Svensk. Vetensk.-Akad. Handl., (3), **20**, no. 1, p. 10.

*Diagnosis.—Homalaspidella* includes small Poraspidinae with shields moderately narrow (width ratio=.43–.54), rather uniform in breadth, and little vaulted. The rostrum is broadly rounded and lacks any median lobe (fig. 146,B). The preorbital processes and orbital notches are slightly developed (fig. 146,A), and the preorbital length is short (orbital ratio=.10–.14). The postbranchial lobes of the dorsal shield are short. Dentine ridges are of moderate width (5–7½ per mm.) and are mostly flat-topped. Epitega are little or not at all indicated, and the ridge pattern (figs. 145, 147) is essentially longitudinal, except for a belt of ridges that runs parallel to the anterior and lateral edges, and for fanned or irregular ridges anteriorly on the ventral shield. The dorsal transverse commissures of the lateral line system are poorly developed.

*Discussion.—Homalaspidella* is quite similar to *Poraspis.* The latter may be distinguished in its dorsal shield by the longer preorbital region (orbital ratio=.14–.20), stronger development of the preorbital processes and orbital notches, narrowing of the dorsal shield in front of the orbits, and longer postbranchial lobes. The simple, essentially longitudinal ridge pattern of *Homalaspidella,* and the absence of indications of epitega is not typical for *Poraspis,* though it is approached by some specimens.

**Homalaspidella nitida** (Kiaer). Figures 98,D, 99,C, 144.

*Homalaspis nitida* Kiaer, 1932, Skr. Svalbard Ishavet, **52**, p. 14, text fig. 6, pl. 4, fig. 1.

*Homaspis nitidus* Kiaer and Heintz, 1935, Skr. Svalbard Ishavet, **40**, pp. 128–132, text-figs. 55–57, pls. 30, 31, fig. 2, pl. 32, fig. 1, pl. 33, fig. 1, pl. 34, fig. 6, pl. 40; Holmgren, 1942, K. Svensk. Vetensk.-Akad. Handl., (3), **20**, no. 1, p. 10.

*Homaspis nitida* Säve-Söderbergh, 1941, Zool. Bidr. Uppsala, **20**, fig. 6 (p. 533).

*Homalaspidella nitida* Flower and Wayland-Smith, 1952, Bull. Mus. Comp. Zool., **107**, p. 361; Stensiö, 1958, Traité de Zool., **13**, fasc. 1, figs. 180B, 203B; Denison, 1963, Fieldiana: Geol., **14**, no. 7, pp. 123–126.

*Type.*—Paleontologisk Museum, Oslo, D 156, dorsal shield (fig. 144).

*Occurrence.*—Early Devonian (Gedinnian), Ben Nevis division, Red Bay series, Spitsbergen.

*Diagnosis.*—The length of the dorsal shield is 20–26 mm., and the orbital ratio is .14. The rostral margin is broadly rounded, and the posterior edge of the dorsal shield is produced into a rounded median lobe. There are about 7 dentine ridges per millimeter, and a broad, flat pineal macula is present.

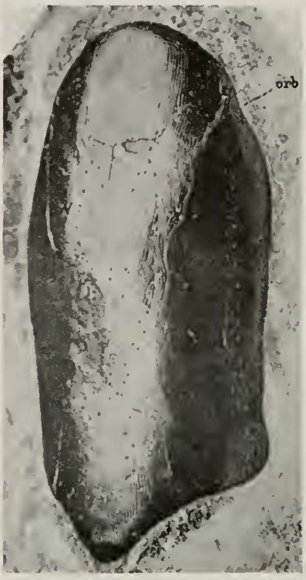

Fig. 144. *Homalaspidella nitida*, type (from Kiaer, 1932); dorsal shield, Paleontologisk Museum, Oslo, D 156 (× 3).
*orb*, orbit.

*Discussion.*—The diagnosis includes var. *robusta* (Kiaer and Heintz, 1935, p. 132), which differs from typical *H. nitida* only in its slightly larger size (length of dorsal shield=23–26 mm.) and broader proportions (width ratio=.54 as compared to .42–.52 in typical forms). Kiaer and Heintz (op. cit., p. 129) indicated that there are only 5 dentine ridges per millimeter, but measurements of their figures and a cast of the type show about 7. Their reconstruction of the dorsal lateral line pattern (fig. 98,D) shows that the dorsal transverse commissures were reduced, but that the longitudinal canals were continuous. In the ventral shield (fig. 99,C), the postoral canals continue into medial ventral canals, the latter appearing, anteriorly at least, as longitudinal canals rather than as transverse commissures. This species is not far removed from *Poraspis*, with which it is associated in the Spitsbergen deposits.

**Homalaspidella borealis** Denison. Figures 145–147.

*Homalaspidella borealis* Denison, 1963, Fieldiana: Geol., **14**, no. 7, pp. 123–127, figs. 70–73.

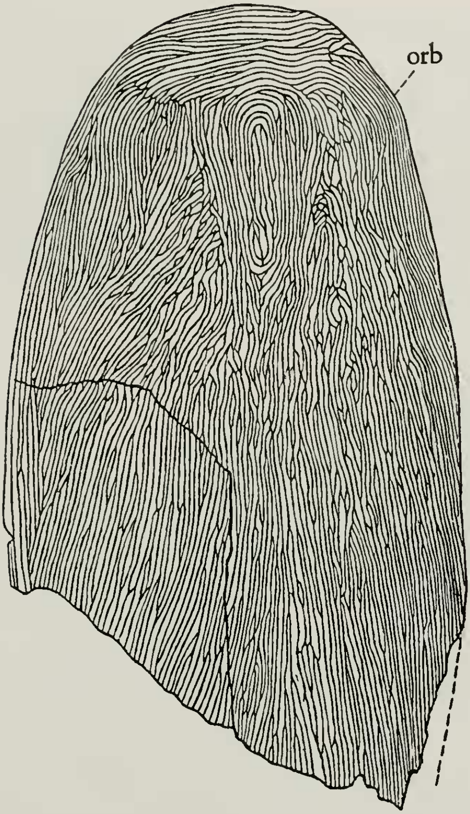

FIG. 145. *Homalaspidella borealis*, type (from Denison, 1963); dorsal shield incomplete posteriorly, Princeton 17101 (× 4).
*orb*, orbit.

*Type.*—Princeton 17101, a dorsal shield, incomplete posteriorly (figs. 145, 146,B).

*Referred specimens:* Princeton 17092, 17102, 17378–17383.

*Occurrence.*—Probably Early Devonian (Early Downtonian) limestones and graptolitic shales,[1] Beaver River, southeastern Yukon.

*Diagnosis.*—The length of the dorsal shield is 28–30 mm., and the orbital ratio is .10–.12. The rostral margin is nearly transverse, and the posterior edge of the shield is gently convex with no median lobe. There are 5.0–6.2 dentine ridges per millimeter. A pineal macula is lacking.

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[1] Tentatively assigned to the Middle Ludlovian in Denison (1963); see below pp. 450–451

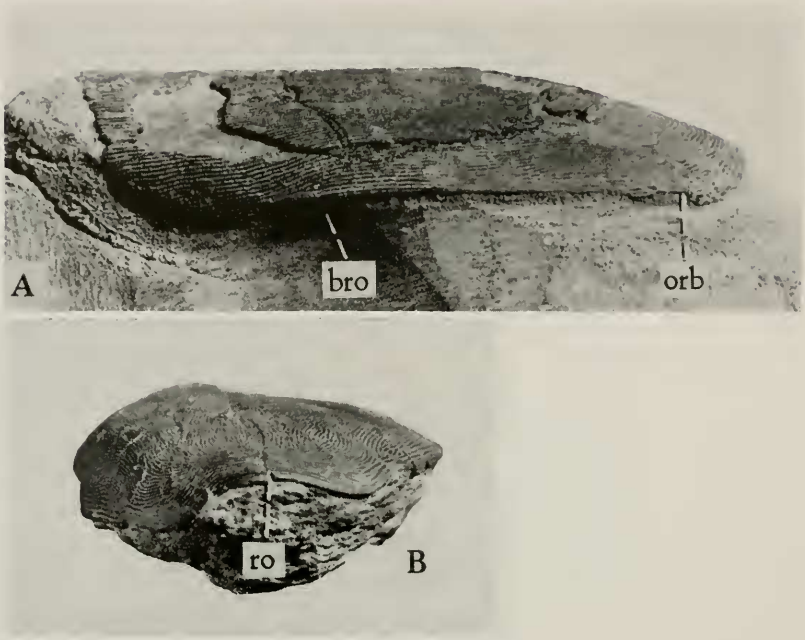

FIG. 146. *Homalaspidella borealis*, dorsal shield (× 3). A, lateral view of right side, Princeton 17379; B, rostral view of type, Princeton 17101.
*bro*, branchial opening; *orb*, orbit; *ro*, rostrum.

*Discussion.*—Though older than *H. nitida*, this species appears to be more advanced in the simplification of the dorsal shield outlines and of the dentine ridge pattern. The orbital notches and preorbital processes (fig. 146,A) are so slightly developed that it is difficult at first to recognize a dorsal shield by its shape. In addition, the absence of epitega and of a pineal macula, and the presence of longitudinal ridges covering most of the shield (fig. 145), make recognition even more difficult. The transverse commissures and medial longitudinal canals of the dorsal sensory line system are divided into short lengths. The ventral shield (fig. 147) is 25–29 mm. long, and has a width ratio of .58. Its ridge pattern resembles that of the dorsal shield: there are a few anterior transverse ridges that continue around to the lateral margins, and the central ridges are longitudinal, becoming irregular behind the anterior transverse ridges.

### Ariaspis Denison

*Type-species.*—*Ariaspis ornata* Denison.

*Ariaspis* Denison, 1963, Fieldiana: Geol., **14**, no. 7, pp. 120–123, 140.

*Diagnosis.*—The dorsal shield is relatively broad and weakly vaulted. There is no median process on the rostral margin, but the preorbital processes are strongly developed. Narrow, downwardly directed lateral laminae extend from the orbits to the branchial openings and are separated from the rest of the shield by sharp angulations. There are no postbranchial lobes, and the postero-lateral corners of the shield are small points. The posterior edge of the dorsal shield is nearly transverse except for a small, median, projecting scale that is incorporated. No epitega are distinguishable.

FIG. 147. *Homalaspidella borealis* (from Denison, 1963); ventral shield, Princeton 17092 (× 4).

**Ariaspis ornata** Denison. Figures 148–149.

*Ariaspis ornata* Denison, 1963, Fieldiana: Geol., **14**, no. 7, pp. 120–123, figs. 68–69.

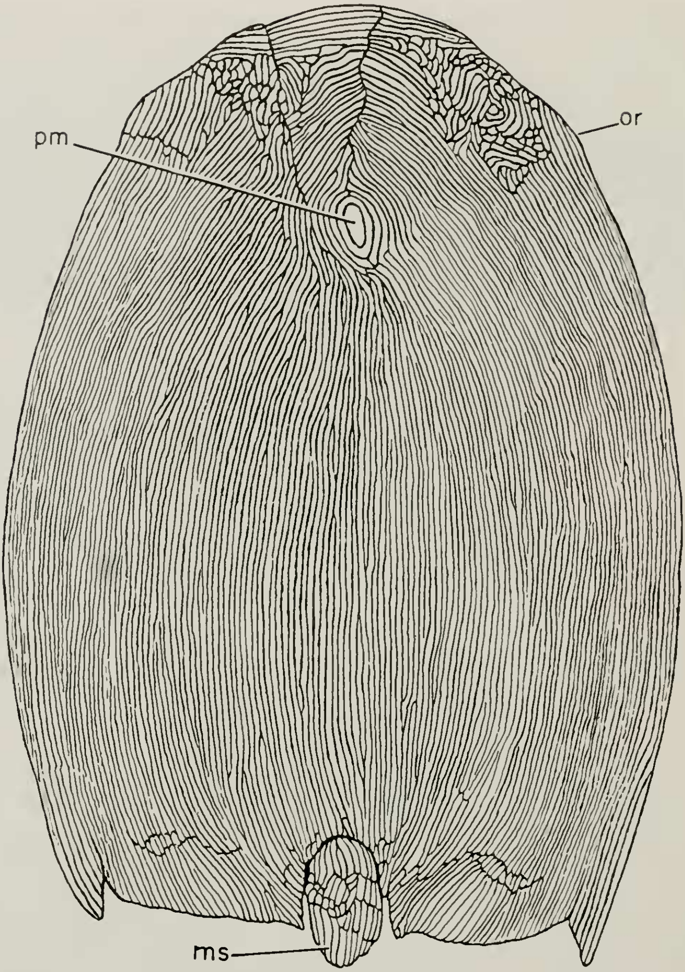

Fig. 148. *Ariaspis ornata*, type (from Denison, 1963); dorsal shield, Princeton 17103 (× 6).

*ms*, median scale; *or*, orbit; *pm*, pineal macula.

*Type.*—Princeton 17103, a complete dorsal shield (figs. 148–149).

*Occurrence.*—Probably Early Devonian (Early Downtonian) limestones and graptolitic shales,[1] Beaver River, southeastern Yukon.

*Diagnosis.*—The length of the dorsal shield is 21.5 mm. The width ratio is .72. The dentine ridges are fine, 7.5–8 per mm., and have sharply or roundly convex crests.

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[1] Tentatively assigned to the Middle Ludlovian in Denison (1963); see (p. 450).

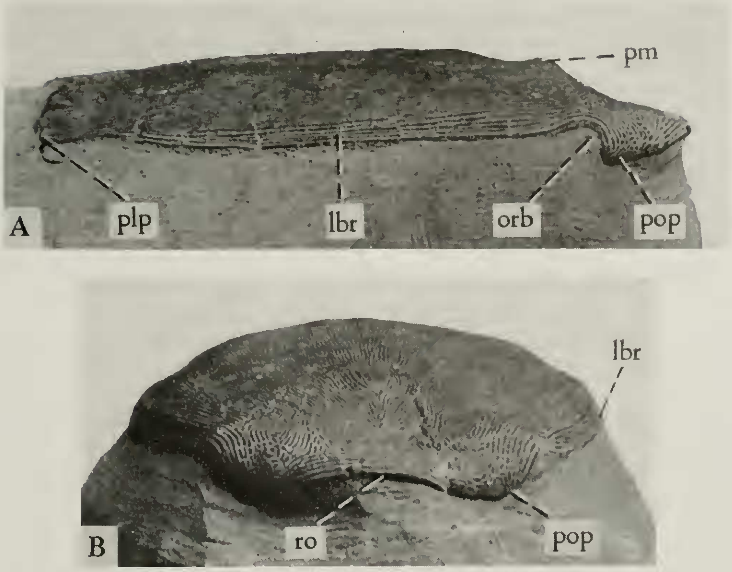

FIG. 149. *Ariaspis ornata*, type; dorsal shield, Princeton 17103 (× 4). A, lateral view of right side; B, rostral view.

*lbr*, lateral lamina; *orb*, orbit; *plp*, postero-lateral point; *pm*, pineal macula; *pop*, preorbital process; *ro*, rostrum.

*Discussion.*—The loss of distinct epitega and the simplification of the ridge pattern are considered to be advanced characters, comparable to the situation in some other Poraspidinae, such as *Homalaspidella* and *Allocryptaspis*. The overall ridge pattern (fig. 148) is elliptical, but is varied by an anterior band of transverse ridges, antero-lateral patches of short, irregular ridges, and a prominent, oval, pineal macula. In addition, there is a break in the continuity of ridges, making it appear as if a pair of large dorso-lateral scales had been fused to the posterior edge. Postero-medially a dorsal ridge scale (fig. 148, *ms*) has been incorporated in and attached to the shield, forming a feature otherwise unknown in Cyathaspididae, though characteristic of Pteraspididae where it is known as the dorsal spine. The lateral laminae of *Ariaspis* (fig. 149, *lbr*) are narrow, ventro-laterally directed bands, probably in no way comparable to the lateral laminae of *Allocryptaspis*, in which they appear to be formed by the fusion of the branchial plates to the dorsal shield. The reduction of the postbranchial lobes and the formation of postero-lateral pointed projections on the dorsal shield are comparable to the situation in *Anglaspis*.

### Anglaspis Jaekel

*Type-species.—Cyathaspis maccullonghi* Woodward.

*Cyathaspis* (in part) Woodward, 1891, Cat. Fossil Fishes Brit. Mus. (Nat. Hist.), **2**, p. 172.

*Anglaspis* Jaekel, 1927, Zeits. Ges. Anat., Abt. 3, Ergebn. Anat. Entwickl., **27**, p. 877; Kiaer, 1932, Skr. Svalbard Ishavet, **52**, p. 20; Holmgren, 1942, K. Svensk. Vetensk.-Akad. Handl., (3), **20**, no. 1, p. 10; Flower and Wayland-Smith, 1952, Bull. Mus. Comp. Zool., **107**, pp. 363–364; Wängsjö, 1952, Skr. Norsk Polarinst., **97**, p. 562; Watson, 1954, Phil. Trans. Roy. Soc. London, (B), **238**, pp. 9–13; Stensiö, 1958, Traité de Zool., **13**, fasc. 1, pp. 314–316, 384–385, 389–391.

*Fraenkelaspis* Stensiö, 1958, Traité de Zool., **13**, fasc. 1, pp. 314–316, 384, 391.

*Diagnosis.—Anglaspis* includes small Poraspidinae in which the dentine ridges are coarse (2½–5 per mm. in the central parts of the shield), and the epitega are quite distinct. The dorsal shield is little arched, but is relatively broad (width ratio=.59–.67); it is constricted at the branchial openings, in front of which the lateral epitega form brims; its postbranchial lobes are very small or absent. The pineal macula is prominent, and the maxillary brim has fine ridges parallel to the margin. The ventral shield is strongly arched posteriorly. The posterior edge of both shields is bluntly pointed. There are no separate postoral plates. The branchial plates have a sharp lateral angulation. The recticular layer is poorly developed, and very large chambers occur in rows in the cancellous layer, one row under each dentine ridge.

*Discussion.*—Certain species of *Anglaspis* have recently been removed by Stensiö (1958) to a new genus, *Fraenkelaspis*, which he distinguished by two features. Firstly, the ventral shield was supposed to have distinct anterior and posterior central hypotega. The ventral shield that Stensiö figures (fig. 150,B in this paper) is the type specimen of *Anglaspis insignis*, and could be interpreted as having the two central hypotega. However, two other ventral shields on the same specimen (Paleontologisk Museum, Oslo, D 186) do not show this division and have a ridge pattern similar to that of typical *Anglaspis*. This case of apparent subdivision of the ventral shield is really nothing but an example of the great individual variability of dentine ridge patterns (cf. Wills, 1935, p. 431, pl. 2). Secondly, Stensiö (1958, pp. 385–386) claims that *Fraenkelaspis* has three vagal visceral arches in contact with the lateral wall of the occipital region, while *Anglaspis* has only two. This interpretation is based, of course, only on the often vague impressions of internal structures on the exoskeleton. Stensiö's reconstruction of *Fraenkelaspis* (op.

cit., fig. 205, B), based on a figure of specimen D 193 in the Paleontologisk Museum in Oslo (Kiaer, 1932, pl. 6, fig. 1), shows important differences from a cast of this specimen in Chicago Natural History Museum (PF 1133). The eighth gill pouch ("$k_9$") is not apparent on the cast, nor is the posterior limit of the visceral endoskeleton ("l. visc. p."). The seventh gill pouch ("$k_8$") is shorter than the fifth and sixth so that the arrangement of the gill pouches is closer to that shown by Stensiö in typical *Anglaspis* (op. cit., fig. 205, A). Stensiö states that his reconstruction of the latter was based on figures of Wills' (1935). However, in his figures and text Wills shows the presence of only seven gills ($k_2$–$k_8$); from his specimens it would be impossible to show definitely that any of them were in contact with the occipital region of the endocranium. There appears to be no justification for the subdivision of *Anglaspis*, and so *Fraenkelaspis* should be discarded.

*Anglaspis* is one of the most distinctive of the Poraspidinae largely because the coarseness of its dentine ridges emphasizes their pattern, and causes the epitega to appear more distinct than in other members of the subfamily. The rostral epitegum and postrostral field are not differentiated. The ridges radiate on the rostro-postrostral area, are nearly longitudinal on the central epitegum, and diagonal on the lateral epitega. On the ventral shield, the ridges typically radiate in the anterior region and are nearly longitudinal in the central area; in the lateral areas they are parallel to the margin.

**Anglaspis macculloughi** (Woodward). Figures 98,B, 102,D.

*Cyathaspis macculloughi* Woodward, 1891, Cat. Fossil Fishes Brit. Mus. (Nat. Hist.), **2**, pp. 172–173, pl. 9, fig. 4.

*Anglaspis macculloghi* Jaekel, 1927, Zeits. Ges. Anat., Abt. 3, Ergebn. Anat. Entwickl., **27**, p. 877, fig. 26.

*Anglaspis macculloughi* Wills, 1935, Trans. Roy. Soc. Edinburgh, **58**, pp. 429–435, figs. 1–3, pl. 1, figs. 2–12, pl. 2, pl. 3, figs. 3–7, pl. 5, fig. 8, pl. 7, figs. 1–4; Westoll, 1945, Trans. Roy. Soc. Edinburgh, **61**, p. 347, fig. 4A; White, 1946, Quart. Jour. Geol. Soc. London, **101**, pp. 210, 211, 213; Watson, 1954, Phil. Trans. Roy. Soc. London, (B), **238**, fig. 4; Bystrow, 1955, Akad. Nauk. SSSR., Mem. Vol. A. S. Berg, pp. 485–487, figs. 13–15; Stensiö, 1958, Traité de Zool., **13**, fasc. 1, figs. 168A–B, 205; White, 1961, Bull. Brit. Mus. (Nat. Hist.), Geol., **5**, p. 246; Ball and Dineley, 1961, Bull. Brit. Mus. (Nat. Hist.), Geol., **5**, p. 223; Heintz, 1962, Coll. Internat., Centre Nat. Rech. Sci., no. **104**, fig. 8D.

*Type.*—British Museum (Natural History), P 4797, imperfect dorsal shield.

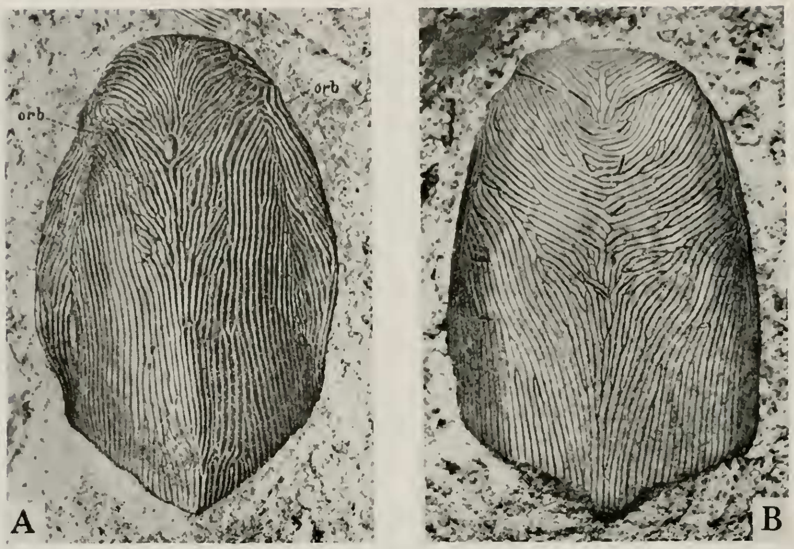

FIG. 150. *Anglaspis insignis* (from Kiaer, 1932); Paleontologisk Museum, Oslo, D 186 (× 3). A, dorsal shield; B, ventral shield, designated as type. *orb*, orbit.

*Occurrence.*—Early Devonian (Late Downtonian), zone of *Traquairaspis symondsi*, Shropshire, Herefordshire, Brecknockshire, and Pembrokeshire, Great Britain. This species is doubtfully reported by White (1950, p. 56) from the Early Dittonian (zone of *Protopteraspis leathensis*) of Worcestershire, England.

*Diagnosis.*—The length of the dorsal shield is 24–30 mm. Centrally there are 2½–3½ dentine ridges per millimeter, and their crests are sharp and high. The orbital ratio is .16–.18, and the pineal ratio is .23–.26.

### **Anglaspis insignis** Wills. Figures 99,B, 150.

*Anglaspis insignis* Kiaer, 1932, Skr. Svalbard Ishavet, **52**, p. 20, pl. 7 (nomen nudum); Wills, 1935, Trans. Roy. Soc. Edinburgh, **58**, pp. 429, 432–433; Denison, 1953, Fieldiana: Geol. **11**, no. 7, p. 292.

*Anglaspis insignis* var. *brevis* Kiaer, 1932, Skr. Svalbard Ishavet, **52**, p. 20, pl. 6, fig. 1 (nomen nudum).

*Fraenkelaspis insignis* Stensiö, 1958, Traité de Zool., **13**, fasc. 1, p. 315, figs. 168C–D, 180A.

*Fraenkelaspis brevis* Stensiö, 1958, Traité de Zool., **13**, fasc. 1, fig. 205B.

*Type.*—Paleontologisk Museum, Oslo, D 186, ventral shield (fig. 150,B).

*Occurrence.*—Early Devonian (Gedinnian), Primaeva, Polaris, Anglaspis, and Red Horizons, Fraenkelryggen division, Red Bay series, Spitsbergen.

*Diagnosis.*—The length of the dorsal shield is 20–23 mm. Centrally there are 3½–5 ridges per millimeter; they are usually flat or slightly convex, but are sharp-crested anteriorly on the rostrum and laterally on the dorsal shield. The orbital ratio is .17 and the pineal ratio is .24.

*Discussion.*—Unfortunately, according to the International Code of Zoological Nomenclature (article 13), the name *Anglaspis insignis* as proposed by Kiaer was a nomen nudum. Wills (1935, p. 429) validated the name when he gave the first "statement that purports to give characters differentiating the taxon."

**Anglaspis heintzi** Heintz. Figures 90, 94,A.

*Anglaspis heintzi* Kiaer, 1932, Skr. Svalbard Ishavet, **52**, p. 20, fig. 11 (nomen nudum); Heintz, 1933, Zeits. Geschiebeforsch., **9**, p. 130, fig. 4; 1962, Coll. Internat., Centre Nat. Rech. Sci., no. **104**, p. 24, fig. 7; Wills, 1935, Trans. Roy. Soc. Edinburgh, **58**, pp. 429, 430, 435; Tarlo, 1962, Acta Paleont. Polonica, **7**, fig. 3.

*Poraspis heintzi* Moy-Thomas, 1939, Palaeozoic Fishes, fig. 2A.

*Fraenkelaspis heintzi* Stensiö, 1958, Traité de Zool., **13**, fasc. 1, fig. 166A.

*Type.*—Paleontologisk Museum, Oslo, specimen not designated.

*Occurrence.*—Early Devonian (Gedinnian), upper part of Fraenkelryggen division, Red Bay series, Spitsbergen.

*Diagnosis.*—The known characters are not sufficient to differentiate this species.

*Discussion.*—*Anglaspis heintzi*, as originally listed by Kiaer, was a nomen nudum. The recent description and figure of the mouth parts by Heintz (1962, p. 24, fig. 7) may be considered as giving "characters differentiating the taxon"; therefore Heintz unwittingly validated the name of a species proposed in his honor.

**Anglaspis elongata** and **A. platostriata**, from the Early Devonian, Red Bay series, Spitsbergen, are nomina nuda, merely listed by Kiaer (1932, p. 20).

**Anglaspis expatriata**, new species. Figure 151.

*Type.*—National Museum of Canada 10038, a nearly complete dorsal shield exposed on the inner side (fig. 151,A).

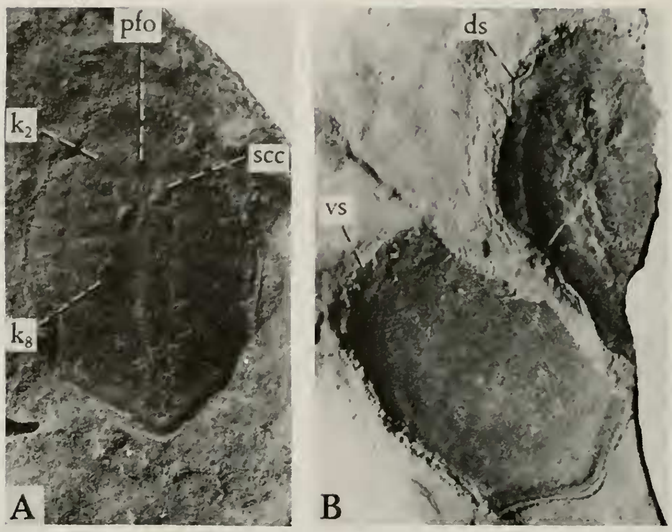

FIG. 151. *Anglaspis expatriata* (× 2). A, rubber impression of type, inner side of dorsal shield, National Museum of Canada 10038; B, ventral shield and part of dorsal shield, inner sides, CNHM, PF 3666.

*ds*, dorsal shield; $k_{2-8}$, impressions of gill pouches; *pfo*, impression of fossa for pineal organ; *scc*, impressions of semicircular canals; *vs*, ventral shield.

*Referred specimens.*—CNHM, PF 3665, a flattened dorsal shield and scales, in counterpart; PF 3666 (fig. 151,B), incomplete dorsal and ventral shields, inner sides; National Museum of Canada, 10039–40, CNHM, PF 3667, incomplete ventral shields; CNHM, PF 3668–69, 3671, shield fragments; PF 3670, scales.

*Occurrence.*—Early Devonian, top of Mt. Sekwi, beside the Keele River, Northwest Territories, Canada (68° 28′ N.; 128° 40′ W.) (California Standard Company locality Z 29–61, 4474′).

*Diagnosis.*—The length of the dorsal shield is about 24 mm., and that of the ventral shield is 20–23 mm. On both shields there are centrally 3–3½ dentine ridges per millimeter, and their crests are sharp and moderately high. The orbits and pineal organ are rather anterior in position; the orbital ratio is .14–.15, and the pineal ratio is .20–.21.

*Discussion.*—*Anglaspis expatriata* is very similar to the British species, *A. macculloughi.* From the latter it differs in its more anterior orbits and pineal organ, and usually in its smaller size. *A. expatriata* may have had rounded postero-lateral corners on the dorsal shield; in *A. macculloughi* these corners form pointed spurs. The maxillary brim of *A. expatriata* is incompletely preserved in PF 3666; it is about 0.7 mm. wide and has approximately 8 fine, even ridges parallel to the anterior margin; in *A. macculloughi* the corresponding ridges appear to be irregular (Wills, 1935, pl. 1, fig. 6, *mb*). In *A. expatriata* (Nat. Mus. Canada 10038) on the inner or ventral surface of the dorsal shield, at the margins where it overlies the branchial openings, there are similar bands, 0.6–0.7 mm. wide, with 6–7 narrow, even dentine ridges; a similar band in *A. macculloughi* (CNHM PF 1390) is shorter, broader (1.2 mm.), and has about 12 ridges of irregular width.

*A. insignis* differs from *A. expatriata* in its somewhat smaller size, in its more posterior orbits and pineal organ, and in its finer dentine ridges, most of which have flat or only slightly convex crests.

The dentine ridge pattern is not well displayed in any of the specimens of *A. expatriata*. On the dorsal shield the ridges are longitudinal posteriorly, but otherwise unknown. On the ventral shield they are longitudinal on the posterior half, and fanned in the anterior third, with two ridges parallel to the antero-lateral and probably anterior edges. PF 3667 shows on the ventral shield a pair of lateral bands of fine ridges (about 6 per mm.) similar to those of *A. macculloughi*.

### **Anglaspis** sp.

*Anglaspis* n. sp. Thorsteinsson, 1958, Geol. Surv. Canada, Mem. **294**, p. 77.

*Occurrence.*—Early Devonian, Snowblind Bay formation, Read Bay, Cornwallis Island, Canada.

*Anglaspis* sp. indet. Gross, 1961, Acta Zool., **42**, pp. 76, 90–96, 143–144, figs. 5,G–K, 6–7.

*Occurrence.*—Downtonian, glacial erratics of red, quartzose Beyrichienkalk, northern Germany.

*Anglaspis* sp. Ball and Dineley, 1961, Bull. Brit. Mus. (Nat. Hist.), Geol., **5**, pp. 202–203, 221, 222, 225, 228, 230, 235.

*Occurrence.*—Early Devonian (Late Downtonian to Middle Dittonian), England.

*Anglaspis* sp. Karatajute-Talimaa, 1962, Lietuvos TSR ma Geologijos ir Geografijos Institutas Moksliniai Pranesimai, Geol.-Geogr., **14**, I sas., pp. 46, 48, 53, 58.

*Occurrence.*—Late Downtonian, boreholes at Krekenava, Staciunai and Papilvis in Lithuania.

cf. *Anglaspis* Thorsteinsson and Tozer, 1963, Geol. Surv. Canada, Mem. **320**, p. 122.

*Occurrence.*—Silurian or Devonian, lower part of Peel Sound formation, 5 miles west of Cunningham Inlet, Somerset Island, Canada.

### Allocryptaspis Whitley

*Type-species.*—*Cryptaspis ellipticus* Bryant.

*Cryptaspis* Bryant (not of Pascoe 1872), 1934, Proc. Amer. Phil. Soc., **73**, p. 154; 1935, Proc. Amer. Phil. Soc., **75**, pp. 112–114; Kiaer and Heintz, 1935, Skr. Svalbard Ishavet, **40**, pp. 132–133.

*Allocryptaspis* Whitley, May 1940, Australian Nat., **10**, p. 243 (new name for *Cryptaspis* Bryant); Denison, 1953, Fieldiana: Geol., **11**, no. 7, p. 294; Stensiö, 1958, Traité de Zool., **13**, fasc. 1, pp. 314–316.

*Bryantaspis* White and Moy-Thomas, June 1940, Ann. Mag. Nat. Hist., (11), **5**, p. 507 (new name for *Cryptaspis* Bryant); Romer, 1945, Vertebrate Paleontology, p. 574.

*Cryptaspidisca* Strand, 1942, Folia Zool. Hydrobiol., **11**, p. 384 (new name for *Cryptaspis* Bryant).

*Diagnosis.*—*Allocryptaspis* includes large Poraspidinae in which the branchial plates are fused to the dorsal shield forming ventrolateral laminae. The branchial openings lie between the dorsal and ventral shields; both shields are notched for these openings (fig. 152,B). The small orbits notch the lateral laminae and are relatively far forward (orbital ratio=.11–.14). The maxillary brim (fig. 92, *mxb*) is small and is ornamented with ridges at right angles to the rostral edge. The postbranchial lobes are short and weakly developed. Both dorsal and ventral shields have a median lobe on the posterior edge. Postoral plates (fig. 95,A–B) are present. The lateral line pattern (figs. 98,E, 99,D) is similar to that of *Poraspis* except that the commissures between the supraorbital and infraorbital lines are absent. Dentine ridges are coarse, 2.3–5 per mm.; their pattern is essentially longitudinal except for fanning in the rostral region and in the anterior part of the ventral shield. No epitega are apparent.

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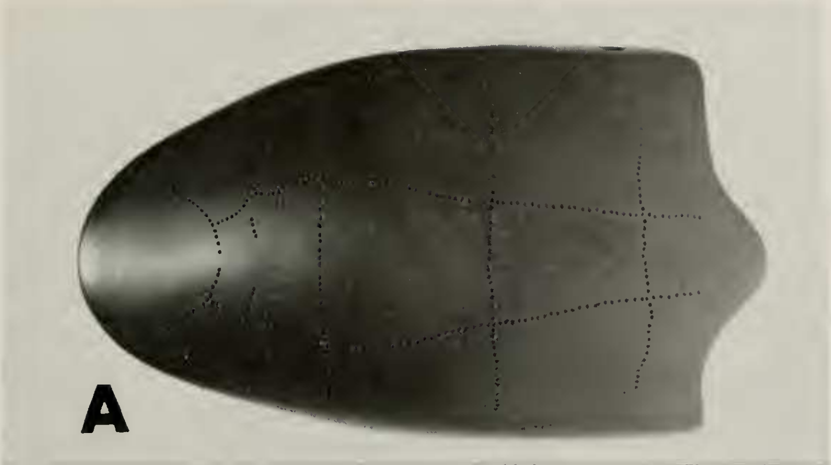
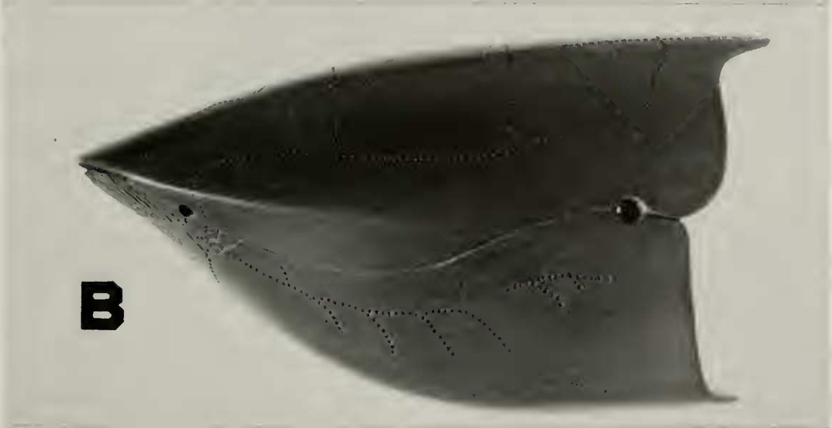
FIG. 152. Restoration of shield of *Allocryptaspis laticostata* (from Denison, 1960); approximately natural size. A, dorsal view; B, lateral view of left side; C, ventral view.



A



B

C

*Discussion.*—In an early paper (Denison, 1953, p. 296) I considered the lateral laminae of *Allocryptaspis* to be differentiated parts of the dorsal shield. In a later paper (Denison, 1960, p. 558) I concluded that these laminae represented the branchial plates that had fused to the dorsal shield. The arguments for the latter hypothesis are as follows: (1) No branchial plates have been found. Those so identified by me (1953, p. 299) are now interpreted as fragments of lateral laminae. The failure to discover branchial plates would ordinarily not be significant, but is in the collection of *Allocryptaspis laticostata* from the Holland Quarry shale, for the abundant material includes specimens of even the smallest oral and lateral plates. (2) The branchial openings notch both the dorsal and ventral shields; therefore, the openings were not bounded by separate branchial plates. (3) Except that they are entirely anterior to the branchial openings, the lateral laminae have the same morphological relations as the branchial plates of typical cyathaspids.

*Allocryptaspis* is the latest, and with the exception of *Ctenaspis* and *Listraspis*, the most specialized member of the Cyathaspididae. Its outstanding specializations are large size, and the fusion of the branchial plates to the dorsal shield with the related modification of the boundaries of the branchial openings. Other advanced characters include: the absence of distinct epitega; the essentially longitudinal pattern of the dentine ridges; the rather complete lateral line pattern; the presence of distinct postoral plates and numerous lateral plates; the thick shields with wide dentine ridges and large chambers arranged in rows in the cancellous layer. *Allocryptaspis* may have been derived from *Americaspis* or *Poraspis*.

### **Allocryptaspis elliptica** (Bryant)

*Cryptaspis ellipticus* Bryant 1934, Proc. Amer. Phil. Soc., **73**, pp. 154–157, fig. 7, pl. 26, fig. 1 (not fig. 8 and pl. 8, fig. 4); 1935, Proc. Amer. Phil. Soc., **75**, pp. 114–118, fig.1, pls. 1–5, pl. 6, fig. 1.

*Allocryptaspis ellipticus* Denison, 1953, Fieldiana: Geol., **11**, no. 7, pp. 295–304, fig. 65A; 1960, Fieldiana: Geol. **11**, no. 10, pp. 556–559.

*Type.*—Princeton 13752, a dorsal shield.

*Occurrence.*—Early Devonian, Beartooth Butte formation, Beartooth Butte, Park County, Wyoming.

*Diagnosis.*—The length of the dorsal shield is 78–91 mm., and that of the ventral shield is 79–83 mm. The shields are narrower than in *A. laticostata* and *A. flabelliformis* (orbital width ratio=.35). There are 4–5 dentine ridges per millimeter, probably smooth-crested.

FIG. 153. *Allocryptaspis utahensis*, ventral view of anterior part of type (from Denison, 1953); dorsal shield, CNHM, PF 737 (× 1).

*brn*, position of notch bounding branchial opening; *ll*, lateral lamina; *or*, orbit.

**Allocryptaspis flabelliformis** (Bryant)

*Cryptaspis flabelliformis* Bryant 1935, Proc. Amer. Phil. Soc., **75**, pp. 118–119, pl. 7.

*Allocryptaspis flabelliformis* Denison 1953, Fieldiana: Geol., **11**, no. 7, pp. 296–299, 304; 1960, Fieldiana: Geol. **11**, no. 10, p. 556.

*Type.*—Princeton 13888, a ventral shield.

*Occurrence.*—Early Devonian, Beartooth Butte formation, Beartooth Butte, Park County, Wyoming.

*Diagnosis.*—The length of the ventral shield is about 100 mm., and it is relatively broad. There are about 4 dentine ridges per mm.

*Discussion.*—This is a poorly characterized species, distinguished by its large size.

**Allocryptaspis laticostata** Denison. Figures 92, 95, 96, 98,E, 99,D, 102,C, 104, 152, 159,B.

*Allocryptaspis laticostatus* Denison, 1960, Fieldiana: Geol., **11**, no. 10, pp. 555–567, figs. 117–123.

*Type.*—CNHM, PF 1701, a dorsal shield (Denison, 1960, fig. 117,A).

*Occurrence.*—Early Devonian, Holland Quarry shale, Holland Quarry, Monclova Township, Lucas County, Ohio.

*Diagnosis.*—The length of the dorsal shield is 81–92 mm., and that of the ventral shield is 81–87 mm. The shields are relatively broader than in other species (orbital width ratio=.41). The dentine ridges are very coarse, 2.3–2.8 per mm., generally flat-topped and finely tuberculate.

**Allocryptaspis utahensis** Denison. Figure 153.

*Allocryptaspis utahensis* Denison 1953, Fieldiana: Geol., **11**, no. 7, pp. 294–304, figs. 61–64, 65,B; 1960, Fieldiana: Geol., **11**, no. 10, pp. 556–559, 564.

*Type.*—CNHM, PF 737, associated dorsal and ventral shields and scales (fig. 153).

*Occurrence.*—Early Devonian, Water Canyon formation, Cottonwood, Green, and Blacksmith Fork Canyons in the Bear River Range, and Dry Lake on the eastern edge of the Wellsville Range, all in Cache County, Utah.

*Diagnosis.*—The length of the dorsal shield is about 110 mm., and that of the ventral shield is about 91 mm. The shields are more slender than in the other species (orbital width ratio=.32). There are 3.2–3.6 dentine ridges per millimeter, with their crests smooth and slightly convex.

## Ctenaspidinae

There is no subdivision of the shield into epitega. The superficial layer is typically absent, and the ornamentation consists of tubercles or an irregular network of ridges. The branchial plates are believed to be fused to the dorsal shield. Postbranchial lobes are absent, and the branchial openings lie between the postero-lateral corners of the dorsal and ventral shields. *Ctenaspis.*

**Ctenaspis** Kiaer

*Type-species.*—*Ctenaspis dentata* Kiaer.

*Ctenaspis* Kiaer, 1930, Skr. Svalbard Ishavet, **33**, pp. 3–5; 1932, Skr. Svalbard Ishavet, **52**, p. 20; Zych, 1931, Fauna Ryb Dewonu i Downtonu Podola, pp. 19, 30, 58, 74, 87; Gross, 1935, Palaeontogr., **83A**, p. 11, Føyn and Heintz, 1943, Skr. Norges Svalbard Ishavs-Undersøk., **85**, p. 42; Flower and Wayland-Smith, 1952, Bull. Mus. Comp. Zool., **107**, p. 364; Denison, 1953, Fieldiana: Geol., **11**, no. 7, p. 293; Stensiö, 1958, Traité de Zool., **13**, fasc. 1, pp. 295, 318–319, 369, 384, 386, 387, 394.

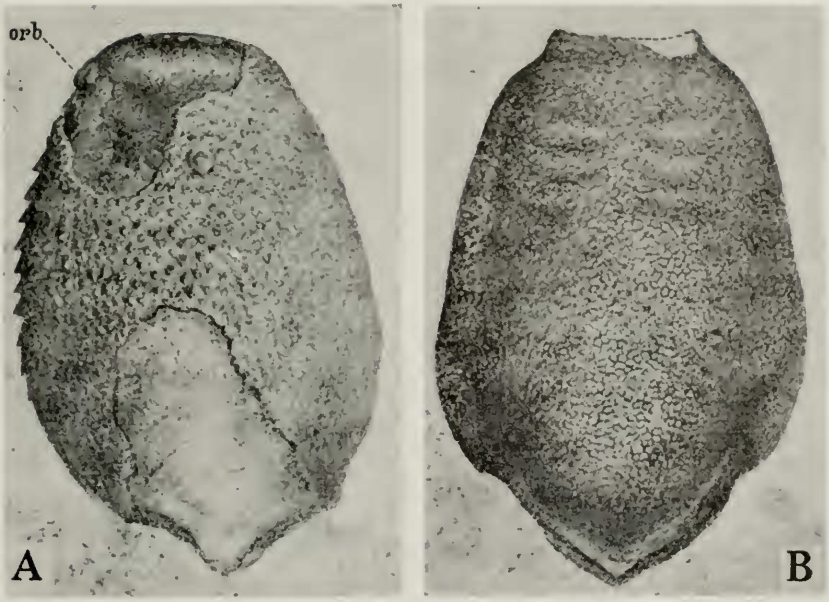


FIG. 154. *Ctenaspis dentata* (× 3). A, type, dorsal shield, Paleontologisk Museum, Oslo, D 582; B, ventral shield. (From Kiaer, 1930.) *orb*, orbit.

*Diagnosis.*—*Ctenaspis* includes Ctenaspidinae in which the shield is short and relatively very broad (width ratio=.70–.90). The dorsal shield is rather flat, has the orbits far forward (orbital ratio=.08–.12), and has well-developed lateral brims. The ventral shield is more strongly arched, except for flatter marginal areas.

*Discussion.*—The presence or absence of distinct branchial plates has not been clearly demonstrated in *Ctenaspis*. Kiaer (1930, p. 4) merely stated that "free branchial plates have not yet been found . . ." Stensiö does not discuss the matter in his text, but in a reconstruction of *Ctenaspis kiaeri* (1958, fig. 176) each side of the dorsal shield is shown to have a ventro-lateral lamella which "représente peut-être la plaque branchiale." The branchial opening is shown behind the posterior end of the lamella at the postero-lateral corner of the shield, and is bounded above by the dorsal shield and below by the ventral shield. The situation is essentially the same as that of *Allocryptaspis*, except that *Ctenaspis* lacks postbranchial lobes and has a marked, toothed brim separating the dorsal face of the shield from the ventro-lateral lamella. I have been able to confirm the presence of the ventro-lateral lamellae and the position of the branchial openings on a specimen of *Ctenaspis dentata* (CNHM, PF 1088, fig. 155). It shows on the ventral surface of the dorsal shield behind the lamella an ornamentation of a few fine ridges, presumably of dentine, overlying the branchial opening.

Though the orbits are far forward, the pineal organ is rather far back (pineal ratio=.23–.27). Preorbital processes are well developed, and between them is a flat maxillary brim (fig. 155, *mxb*), ornamented with denticles and ridges (presumably of dentine) parallel to the rostral edge. Some species have dorsally a postero-median crest which is part of the dorsal shield and not a separate element as is the dorsal spine of pteraspids. The lateral line pattern (figs. 97,D, 99,F) shows some differences from the typical cyathaspid arrangement which Kiaer (1930, p. 3) believed approached the pteraspid condition. The posterior ends of the supraorbital canals (=pineal canals) meet behind the pineal macula. Only two or three dorsal transverse commissures are present. Paired medial ventral canals are continuous with the postoral canals and extend about half way back on the ventral shield. A thin section of *Ctenaspis dentata* (PF 1088, fig. 101,C) shows that the superficial layer is absent. The surface ornament consists of tubercles of aspidine, and this is probably true also of other described species of *Ctenaspis*.

### **Ctenaspis dentata** Kiaer. Figures 97,D, 99,F, 101,C, 154, 155.

*Ctenaspis dentata* Kiaer, 1930, Skr. Svalbard Ishavet, **33**, p. 7, figs. 1, 2, 4a; 1932, Skr. Svalbard Ishavet, **52**, p. 20; Zych, 1931, Fauna Ryb Dewonu i Downtonu Podola, drawings 29–30; Stensiö, 1958, Traité de Zool., **13**, fasc. 1, p. 295, fig. 177; Friend, 1961, Proc. Yorkshire Geol. Soc. **33**, pt. 1, no. 5, p. 112.

*Type.*—Paleontologisk Museum, Oslo, D 582, dorsal shield (fig. 154,A).

*Occurrence.*—Early Devonian (Gedinnian), Ben Nevis (and ? Fraenkelryggen) division, Red Bay series, Spitsbergen.

*Diagnosis.*—The length of the dorsal shield is 25–27 mm., its width ratio is about .80, and its lateral brims are finely serrate. The surface ornament consists of large, flat tubercles, pointed toward the rear.

### **Ctenaspis cancellata** Kiaer

*Ctenaspis cancellata* Kiaer, 1930, Skr. Svalbard Ishavet, **33**, p. 7, fig. 4*b*; Stensiö, 1958, Traité de Zool., **13**, fasc. 1, p. 295; Friend, 1961, Proc. Yorkshire Geol. Soc., **33**, pt. 1, no. 5, p. 112.

*Ctenaspis conselatus* (in error) Kiaer, 1932, Skr. Svalbard Ishavet, **52**, p. 20.

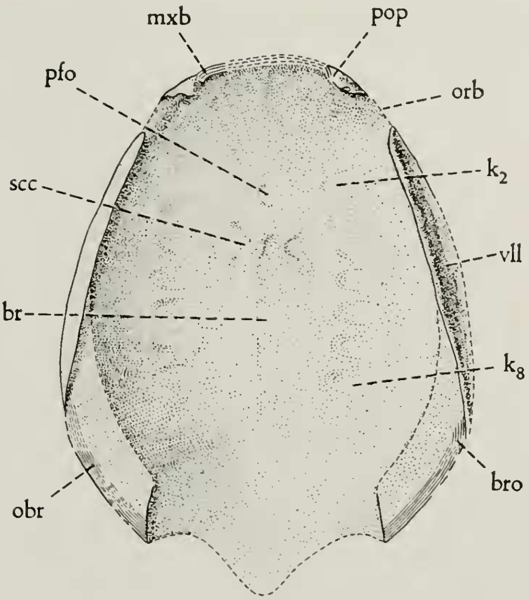


FIG. 155. *Ctenaspis dentata*, ventral view of dorsal shield based largely on CNHM, PF 1088 (× 3); impressions on inner side of central part largely from Kiaer, 1930.

*br*, impression of cranial cavity; *bro*, branchial opening; $k_{2-8}$, impressions of gill pouches; *mxb*, maxillary brim; *obr*, ornamented border of branchial opening; *orb*, orbit; *pfo*, fossa for pineal organ; *pop*, preorbital process; *scc*, impression of semicircular canal; *vll*, ventro-lateral lamina.

*Type.*—Paleontologisk Museum, Oslo, D 543a.

*Occurrence.*—Early Devonian (Gedinnian), Ben Nevis division, Red Bay series, Spitsbergen.

*Diagnosis.*—The length of the dorsal shield is about 30 mm., its width ratio is about .90, and the lateral brims are coarsely serrate. The surface ornament consists of rounded tubercles, more widely spaced than in *C. dentata*.

### **Ctenaspis kiaeri** Zych

*Ctenaspis kiaeri* Zych, 1931, Fauna Ryb Dewonu i Downtonu Podola, photo 11, drawings 45*a–e;* Kiaer, 1932, Skr. Svalbard Ishavet, **52**, p. 20; Brotzen, 1936, Ark. Zool., **28A**, no. 22, p. 6; Stensiö, 1958, Traité de Zool., **13**, fasc. 1, p. 295, figs. 176, 178.

*Lectotype.*—Naturhistoriska Riksmuseet, Stockholm, C1616, dorsal shield (according to Stensiö, 1958, fig. 176; not designated by Zych).

*Occurrence.*—Early Devonian (Gedinnian), passage beds of Czortków stage, Podolia.

*Diagnosis.*—The length of the dorsal shield is about 23 mm., its width ratio is about .70, and its lateral brims are only faintly serrate. The surface ornament consists of a network of delicate ridges.

### **Ctenaspis zychi** Stensiö

*Ctenaspis zychi* Stensiö, 1958, Traité de Zool., **13**, fasc. 1, p. 295 (nomen nudum, listed as a new species from Podolia).

### **Ctenaspis** sp.

*Ctenaspis* n. sp. aff. *C. dentatus* Kiaer, Thorsteinsson, 1958, Geol. Surv. Canada, Mem. **294**, pp. 76–77.

*Occurrence.*—Early Devonian, Snowblind Bay formation, Read Bay, Cornwallis Island, Canada.

cf. *Ctenaspis* sp. Wills, 1935, Trans. Roy. Soc. Edinburgh, **58**, pp. 428–429, pl. 1, fig. 1; White, 1946, Quart. Jour. Geol. Soc., London, **101**, p. 210.

*Occurrence.*—Early Devonian (Late Downtonian), zone of *Traquairaspis symondsi*, Shropshire, England.

*Ctenaspis* Føyn and Heintz, 1943, Skr. Norges Svalbard Ishavs-Undersøk., **85**, pp. 43, 44; Friend, 1961, Proc. Yorkshire Geol. Soc., **33**, pt. 1, no. 5, p. 111.

*Occurrence.*—Early Devonian (Gedinnian), Fraenkelryggen division, Red Bay series, Spitsbergen.

## **Cyathaspididae** indet.

## INDETERMINABLE CYATHASPIDIDAE FROM EASTERN UNITED STATES

### **Eoarchegonaspis wardelli** Ruedemann

*Anatifopsis wardelli* (in part) Ruedemann, 1916, Bull. N. Y. State Mus., **189**, pp. 102–105, pl. 32, fig. 2.

*Eoarchegonaspis wardelli* (in part) Kiaer, 1932, Skr. Svalbard Ishavet, **52**, p. 24; Flower and Wayland-Smith, 1952, Bull. Mus. Comp. Zool., **107**, p. 370, pl. 2, fig. 5.

*Lectotype.*—New York State Mus. 9613.

*Occurrence.*—Late Silurian, Otisville Shale member of Shawangunk formation, near Otisville, Orange County, New York.

*Discussion.*—The taxonomic and nomenclatorial problems related to this species have been considered above (p. 374) in the dis-

FIG. 156. "*Archegonaspis*" *drummondi*, type; internal impression of dorsal shield, Museum of Comparative Zoology 8875 (× 3).

$k_{2-8}$, impressions of gill pouches; *pfo*, fossa for pineal organ; *scc*, impression of semicircular canal.

cussion of *Vernonaspis vaningeni*. Since Flower and Wayland-Smith have designated an unrecognizable fragment as lectotype, this name becomes a *nomen dubium* and further use of it becomes impracticable.

**"Archegonaspis" drummondi** Flower and Wayland-Smith. Figure 156.

*Archegonaspis drummondi* Flower and Wayland-Smith, 1952, Bull. Mus. Comp. Zool., **107**, pp. 380–381, pl. 2. figs. 1–2.

*Archegonaspis* cf. *drummondi* Flower and Wayland-Smith, 1952, Bull. Mus. Comp. Zool., **107**, pp. 381–382, pl. 6.

*Archegonaspis* ? sp. Flower and Wayland-Smith, 1952, Bull. Mus. Comp. Zool., **107**, pp. 382–384, fig. 2, pl. 3, fig. 6, pl. 7, pl. 8. fig. 3.

*Type.*—Museum of Comparative Zoology 8875, impression of the inner side of a dorsal shield (fig. 156).

*Occurrence.*—Late Silurian, Vernon shale (Salina group); 2 miles southeast of Kenwood, Oneida County, New York.

*Discussion.*—In the type specimen, the length of 22.1 mm. indicates a considerably smaller species than the others from the Vernon shale, *Vernonaspis allenae* and *V. leonardi.* It resembles *Archegonaspis* and differs from *Vernonaspis* in the following characters: (1) it is relatively broad (width ratio=.64), but its breadth has probably been increased by flattening; (2) the pineal organ and orbits are placed rather posteriorly, but the ratios have probably been altered slightly by measuring on an internal impression; the pineal ratio=.24 and the orbital ratio=.14. It resembles *Vernonaspis* and differs from *Archegonaspis* in having median lobes on the rostral and posterior margins. The dentine ridges, indicated by a small patch on one postbranchial lobe and by impressions along the posterior margin, are very fine, about 8 per mm. The postbranchial lobes are weak and the postbranchial region is shorter than in *Archegonaspis* and *Vernonaspis.* Seven pairs of gill pouches are indicated, corresponding to those numbered $k_2$–$k_8$ by Stensiö (1958).

The ventral shield impression (Mus. Comp. Zool. 8876) identified as *Archegonaspis* cf. *drummondi* by Flower and Wayland-Smith, agrees in size (length given as 21 mm.) and in its fine dentine ridges (about 8 per mm.). The dentine ridge pattern is essentially longitudinal, except that in front the ridges curve toward the anterolateral corners. Its outline is not completely preserved so its original shape is unknown.

The ventral shield in counterpart (Mus. Comp. Zool. 8877) named *Archegonaspis*? sp. by Flower and Wayland-Smith, can also be referred to "*Archegonaspis*" *drummondi.* It is small; its total length is estimated to be 19.5 mm. (not 24 mm. as given in the original description). The shield is badly crushed and its proportions are not determinable. The "eccentric emargination of the anterior end" is the result of a break and is not a natural character. The posterior edge has a very slight rounded median lobe. The ridges are fine, about 8 per mm. The ridge pattern is similar to that of MCZ 8876. This specimen has been etched by the original describers and displays much of the pattern of the lateral line canals. It differs from the typical cyathaspid pattern, as exemplified by *Poraspis,* in that the lateral ventral canals are broken into short lengths and the medial ventral lines appear as transverse commissures showing a gradual transition anteriorly into the postoral canals.

Although this is surely a valid species, none of the three specimens is adequate to determine its generic affinities. Possibly it is identical with *Vernonaspis bryanti.*

*Heterostraci plates.*—Leutze (1960, p. 215). This record was based on scales, now PF 2131–2 in Chicago Natural History Museum, from the Late Silurian, Wills Creek formation, on the east side of Elkhorn Mountain, near Bass, Hardy County, West Virginia.

*Fish scales.*—Hoskins (1961, p. 98, pl. 7, fig. 2). These fragments have been found in the Late Silurian, Bloomsburg formation, at Beavertown in Snyder County, Mifflintown in Juniata County, Strodes Mills, Pine Glen and Mt. Union in Mifflin County, and Neffs Mills in Huntingdon County, Pennsylvania. They were compared by Hoskins to cyathaspids from eastern Pennsylvania identified by Beerbower and Hait (1959) as *Archegonaspis van ingeni* (here referred to *Vernonaspis vaningeni*).

## INDETERMINABLE CYATHASPIDIDAE FROM THE YUKON, CANADA

*Undetermined Cyathaspididae.*—Denison (1963, pp. 127–132, figs. 74–77). The Early Devonian[1] limestones and graptolitic shales on the Beaver River in the southeastern Yukon have yielded, in addition to the species described above, a number of cyathaspids that are too incomplete or poorly preserved to warrant designation by name. A dorsal shield, Princeton 17384 (op. cit., fig. 74), is of interest because of its superficial subdivision into a central disc, a lateral epitegum, a postero-lateral area, and a scale-like band along the posterior border. Another dorsal shield, Princeton 17385, is notable for its great relative breadth, its width ratio being 0.77. A fragment of a ventral shield, Princeton 17094, is characterized by distinct anterior and lateral marginal areas, and by fine ridges. Another ventral shield (fig. 157), Princeton 17387 (op. cit., figs. 75–76), has a dentine ridge pattern resembling that of pteraspids, though its lateral line sensory canals are arranged as in cyathaspids. Two other ventral shields, Princeton 17093 and 17386, are indeterminable, though the latter may belong to *Poraspis*. Finally a branchial plate, Princeton 17099 (op. cit., fig. 77), could belong to *Vernonaspis bamberi*.

*Poraspidinae indet.*—A new locality discovered in 1963 by California Standard Company geologists near the Snake River in northern Yukon, has yielded, in addition to the ?*Dinaspidella* sp. described above (p. 400), two other cyathaspids. One (CNHM, PF 3872) is a ventral shield of a small member of the Poraspidinae. Its age is probably Early Devonian.

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[1] Tentatively assigned to the Middle Ludlovian in Denison (1963); see below pp. 450–451

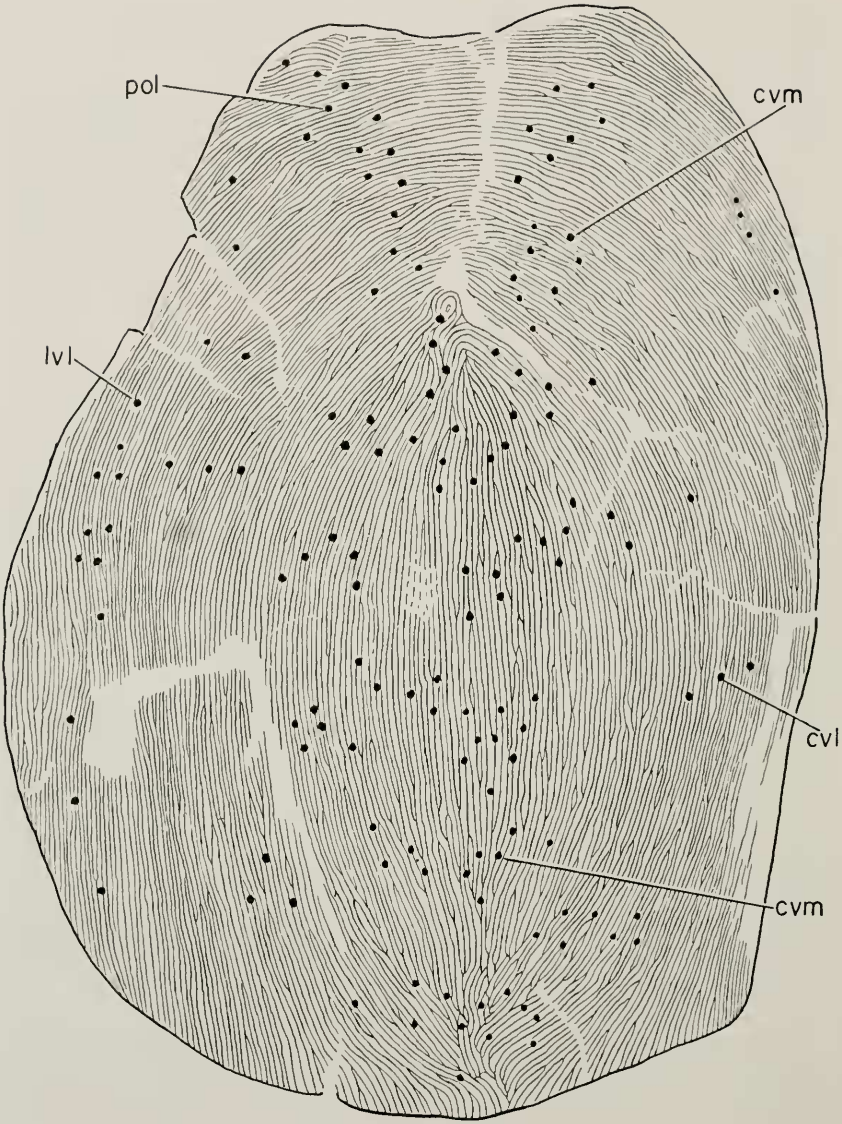


FIG. 157. Cyathaspid indet.; ventral shield, Princeton 17387 (× 2).

*cvl*, *cvm*, pores of lateral and medial ventral transverse sensory commissures; *lvl*, pores of lateral ventral sensory canal; *pol*, pores of postoral sensory canal.

*Cyathaspidinae indet.*—From the same locality in the northern Yukon, a shield fragment (CNHM, PF 3873) shows larger and higher dentine ridges interspersed between smaller and lower ridges. This character occurs in a number of Cyathaspidinae.

## UNDESCRIBED CYATHASPIDIDAE FROM ARCTIC CANADA

*Cyathaspididae n. gen. A and sp. B.*—Thorsteinsson (1958, pp. 54, 72, 100). This is listed from the Middle Silurian (Late Wenlockian, zone of *Monograptus testis* and *Cyrtograptus trilleri*) in the Read Bay formation (member A) on Goodsir Creek, and in the Cape Phillips formation (member C) on Snowblind Creek, Cornwallis Island, Canada.

*New genus and species of Cyathaspididae.*—Thorsteinsson (1958, p. 55; 1963, pp. 227–228). This is reported from the Late Silurian (Early Ludlovian), Read Bay formation (member A), on Shellabear Creek, Cornwallis Island, from the Douro formation, near Ptarmigan Lake, Douro Range, Devon Island, Canada.

*Cyathaspididae gen. and sp. indet.*—Thorsteinsson (1958, p. 68). This is listed from the Late Silurian (? Middle Ludlovian), Read Bay formation (member C), at the head of Snowblind Bay, Cornwallis Island, Canada.

*Cyathaspididae gen. and sp. indet.*—Thorsteinsson (1958, p. 77). This occurs in the Snowblind Bay formation on Read Bay, Cornwallis Island, Canada. Its age is probably Early Devonian.

*Porapsinae* [sic].—Thorsteinsson and Tozer (1963, p. 122). This is listed from the Late Silurian or Devonian, Peel Sound formation, 6 miles southeast of Cape Anne, Somerset Island, Canada.

## INDETERMINABLE FRAGMENTS FROM NORTHERN EUROPE

*Cyathaspidés.*—Lehman (1937, pp. 62–64, pl. 8, figs. 85–88). This record is based on a shield fragment resembling *Cyathaspis* in having higher dentine ridges separated by two or three lower and narrower ridges. It came from the latest Silurian or earliest Devonian Öved-Ramsåsa beds in southern Sweden. It has also been figured by Stensiö (1958, fig. 173,C).

*Poraspididae gen. indet.*—Karatajute-Talimaa (1962, pp. 46, 48, 53, 55, 58, text-fig. 1:6, pl. 1, fig. 23). An incomplete scale from a deep borehole in Lithuania is considered to be Early Devonian (Late Downtonian) on the basis of associated fish fragments.

## Fragmentary or questionable Cyathaspididae from Asia

### **Sanidaspis siberica** Bystrow

*Sanidaspis siberica* Bystrow, 1959, Acta Zool., **40**, pp. 59–62, figs. 1–3.

*Occurrence.*—Early Devonian, Krasny Creek, a left tributary of the River Nizhni Viluikan, Siberia (60° 20′ 27″ N.; 107° 01′ 15″ E.).

*Description.*—The shield has coarse, shiny, dentine ridges, each underlain by two pulp canals. The cancellous layer has very large chambers.

*Discussion.*—This genus and species was based on fragments only and its affinities are uncertain. It resembles *Allocryptaspis* in the coarseness of its dentine ridges (.30–.35 mm.), in the thickness of its shield (1.3 mm.), and in having a pair of pulp canals in each ridge. However, *Allocryptaspis* generally has a linear arrangement of chambers in the cancellous layer under each dentine ridge, while there is no correspondence of ridges and chambers in *Sanidaspis*. *Allocryptaspis* has few lateral canals connecting pulp canals and intercostal grooves, while these are numerous in *Sanidaspis*.

### **Kiangsuaspis nankingensis** P'an

New genus of Cyathaspida: P'an, 1961, Vertebrata Palasiatica, **1961**, no. 4, p. 348.

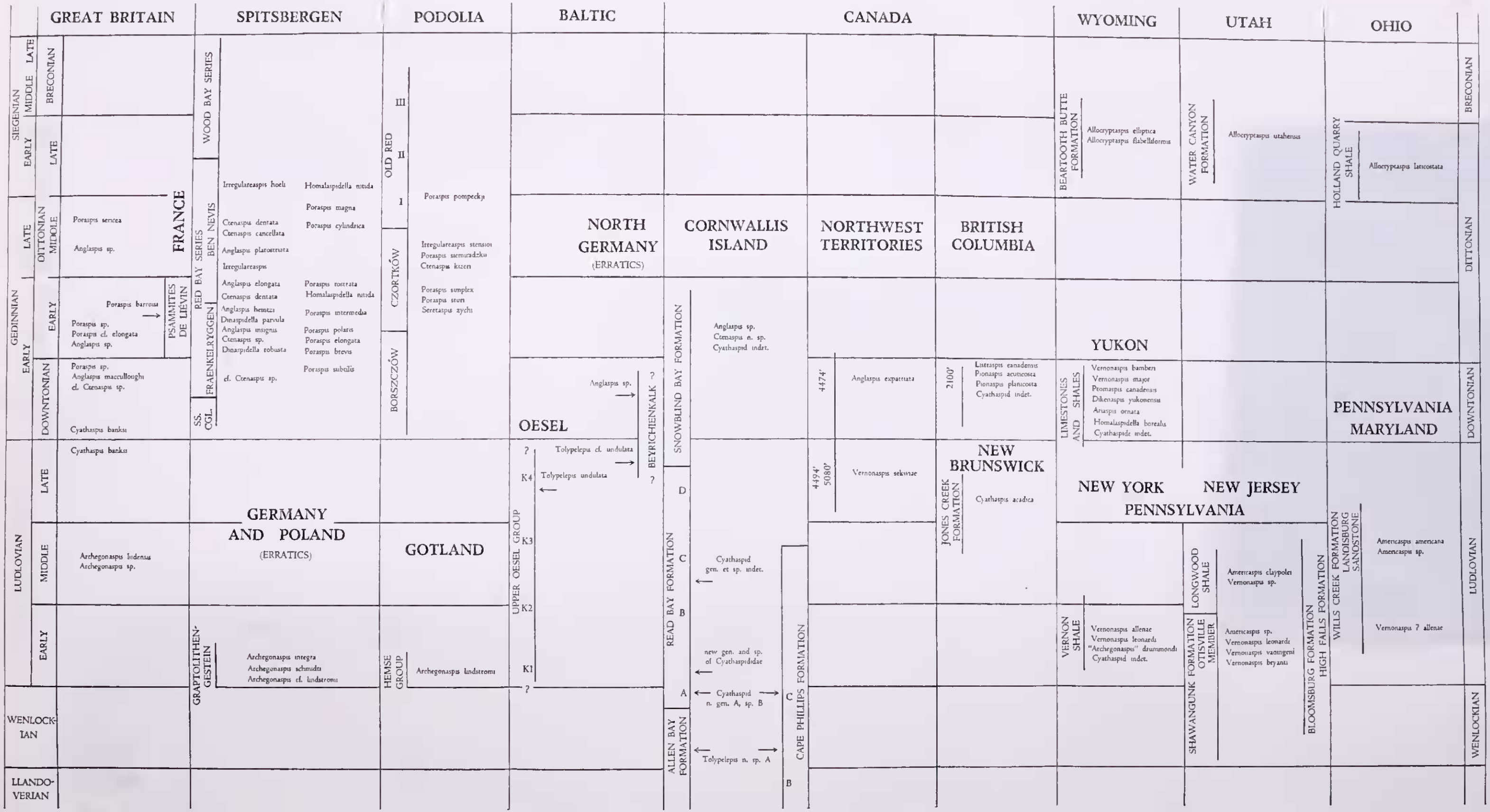
*Kiangsuaspis nankingensis* P'an 1962, Acta Palaeontologica Sinica, **10**, no. 3, pp. 407–408, text-fig. 1A, pl. 1.

*Type.*—Incomplete ventral shield, no. V994, Museum of Geology, Ministry of Geology, Peking.

*Occurrence.*—Possibly Late Silurian, upper part of Fentou series, Fentou, Nanking, Kiangsu Province, China.

*Discussion.*—The ornamentation in the central part of the shield consists of widely spaced coarser and finer ridges, separated by a network of very fine, low ridges, the latter possibly formed by the reticular layer. There is nothing like it in any other cyathaspid. It is possible that *Kiangsuaspis* is related to the Traquairaspididae, though the ridges are not broken into short lengths as is usual in *Traquairaspis*.

FIG. 158. Correlation chart showing occurrence of Cyathaspididae.


GREAT BRITAIN
SPITSBERGEN
PODOLIA
BALTIC
CANADA
WYOMING
UTAH
OHIO
SIEGENIAN
LATE
MIDDLE
EARLY
BRECONIAN
LATE
DITTONIAN
MIDDLE
LATE
EARLY
GEDINNIAN
EARLY
DOWNTONIAN
LUDLOVIAN
LATE
MIDDLE
EARLY
WENLOCKIAN
LLANDOVERIAN
Poraspis sericea
Anglaspis sp.
Poraspis barroisi
Poraspis sp.
Poraspis cf. elongata
Anglaspis sp.
Poraspis sp.
Anglaspis macculloughi
cf. Ctenaspis sp.
Cyathaspis banksi
Cyathaspis banksi
Archegonaspis ludensis
Archegonaspis sp.
FRANCE
PSAMMITES DE LIÉVIN
WOOD BAY SERIES
RED BAY SERIES
BEN NEVIS
FRAENKELRYGGEN
SS. CGL.
Irregulareaspis hoeli
Homalaspidella nitida
Poraspis magna
Ctenaspis dentata
Ctenaspis cancellata
Poraspis cylindrica
Anglaspis plarostrata
Irregulareaspis
Anglaspis elongata
Poraspis rostrata
Ctenaspis dentata
Homalaspidella nitida
Anglaspis heintzi
Poraspis intermedia
Dinaspidella parvula
Anglaspis insignis
Poraspis polaris
Ctenaspis sp.
Poraspis elongata
Dinaspidella robusta
Poraspis brevis
Poraspis subtilis
cf. Ctenaspis sp.
GERMANY AND POLAND
(ERRATICS)
GRAPTOLITHEN-GESTEIN
Archegonaspis integra
Archegonaspis schmidti
Archegonaspis cf. lindstromi
OLD RED
III
II
I
Poraspis pompeckji
CZORTKÓW
Irregulareaspis stensioi
Poraspis siemiradzkii
Ctenaspis kiaeri
Poraspis simplex
Poraspis sturi
Seretaspis zychi
BORSZCZÓW
GOTLAND
HEMSE GROUP
Archegonaspis lindstromi
NORTH GERMANY
(ERRATICS)
Anglaspis sp.
OESEL
BEYRICHIENKALK
?
?
Tolypelepis cf. undulata
Tolypelepis undulata
?
K4
K3
K2
K1
?
UPPER OESEL GROUP
CORNWALLIS ISLAND
SNOWBLIND BAY FORMATION
Anglaspis sp.
Ctenaspis n. sp.
Cyathaspid indet.
READ BAY FORMATION
D
C
B
A
Cyathaspid gen. et sp. indet.
new gen. and sp. of Cyathaspididae
Cyathaspid n. gen. A, sp. B
ALLEN BAY FORMATION
Tolypelepis n. sp. A
CAPE PHILLIPS FORMATION
C
B
NORTHWEST TERRITORIES
4474'
Anglaspis expatriata
4494'
5080'
Vernonaspis sekwiae
BRITISH COLUMBIA
2100'
Listraspis canadensis
Pionaspis acuticosta
Pionaspis planicosta
Cyathaspid indet.
NEW BRUNSWICK
JONES CREEK FORMATION
Cyathaspis acadica
BEARTOOTH BUTTE FORMATION
Allocryptaspis elliptica
Allocryptaspis flabelliformis
WATER CANYON FORMATION
Allocryptaspis utahensis
HOLLAND QUARRY SHALE
Allocryptaspis laticostata
YUKON
LIMESTONES AND SHALES
Vernonaspis bamberi
Vernonaspis major
Promaspis canadensis
Dikenaspis yukonensis
Ariaspis ornata
Homalaspidella borealis
Cyathaspide indet.
PENNSYLVANIA
MARYLAND
NEW YORK
NEW JERSEY
PENNSYLVANIA
VERNON SHALE
Vernonaspis allenae
Vernonaspis leonardi
"Archegonaspis" drummondi
Cyathaspid indet.
SHAWANGUNK FORMATION
LONGWOOD SHALE
OTISVILLE MEMBER
Americaspis claypolei
Vernonaspis sp.
Americaspis sp.
Vernonaspis leonardi
Vernonaspis vaningeni
Vernonaspis bryanti
BLOOMSBURG FORMATION
HIGH FALLS FORMATION
WILLS CREEK FORMATION
LANDISBURG SANDSTONE
Americaspis americana
Americaspis sp.
Vernonaspis ? allenae
BRECONIAN
DITTONIAN
DOWNTONIAN
LUDLOVIAN
WENLOCKIAN

## GEOLOGICAL RANGE

The Cyathaspididae have a rather short geological range. The earliest known member of the family occurs near the base of the Middle Silurian, while the latest occurs below the top of the Early Devonian. The relative ages of most of the species are shown on the accompanying correlation chart (fig. 158). For purposes of correlation the British section is used as a standard, and for the Early Devonian the stage names of the predominantly marine section of the Ardennes and Rheinischen Schiefergebirge are also used. A few of the correlations require some comment.

In the British section the boundary between the Downtonian and Dittonian is here retained between the zone of *Traquairaspis symondsi* and the zone of *Protopteraspis leathensis,* as is common usage (White, 1950, p. 56; Ball and Dineley, 1961, pp. 201–202). Allen and Tarlo (1963, pp. 146–148) have recently argued that the boundary should be placed lower, at the base of the zone of *Traquairaspis pococki.*

The Czortków stage of Podolia has commonly been referred to the Downtonian, and recently certain Russian stratigraphers have placed it in the Tiver stage, which they insert between the typical Ludlovian and Downtonian (Sokolov, 1960; Nikiforowa and Obut, 1962). The pteraspids not only indicate that the age is Dittonian, but that it is Middle Dittonian (Denison, 1956, pp. 403–404; Ørvig, 1961, p. 523). The pteraspids also indicate that the overlying "Old Red" (Babin sandstone) includes Middle Dittonian to Breconian equivalents. A recent review of the invertebrate faunas, particularly the brachiopods (Boucot and Pankiwskyj, 1962), dates the Czortków stage as Early Gedinnian.

The Upper Oesel group of the Island of Oesel in the Baltic has generally been correlated with the Ludlovian, but some workers have argued for an earlier dating (Lamont, 1952, p. 30). Some Russian stratigraphers (Sokolov, 1960, p. 101; Nikiforowa and Obut, 1960, pp. 281–282) place the Upper Oesel group in the Early Ludlovian, but it should be noted that in their usage this corresponds to the entire Ludlovian of the typical section.

Glacial boulders of Beyrichienkalk from northern Germany have been separated into two zones by Gross (1961, pp. 74, 76). The earlier zone is characterized by *Thelodus parvidens* and may be equivalent to the upper or $K_4$ horizon of the Upper Oesel group. In this zone occurs *Tolypelepis* cf. *undulata* (in litt., March 18, 1963). The later zone is characterized by *Thelodus* cf. *scoticus.* This includes the so-called red Beyrichienkalk in which is found *Anglaspis, Corvaspis* and *Traquairaspis,* an assemblage suggestive of Late Downtonian age.

On Cornwallis Island the geology has been described and the faunas listed, but not yet described, by Thorsteinsson (1958). The two cyathaspid-bearing horizons in the upper part of the Cape Phillips formation are dated by graptolites: *Tolypelepis* n. sp. A, found in the zone of *Monograptus riccartonensis* (Early Wenlockian), is the oldest known member of the family; Cyathaspid n. gen. A and sp. B occurs in the zone of *Monograptus testis* and *Cyrtograptus trilleri* (Late Wenlockian). *Tolypelepis* n. sp. A also occurs in the upper part of the Allen Bay formation, which for this reason in part is correlated with the upper part of the Cape Phillips formation. Cyathaspid n. gen. A and sp. B also occurs in the lower part of the Read Bay formation, which is correlated for this and other reasons with the upper part of the Cape Phillips formation. The Read Bay formation also contains a new genus and species of cyathaspid which is dated by brachiopods and graptolites as Early Ludlovian, and an undetermined cyathaspid which is only tentatively dated as Middle Ludlovian. Other cyathaspids have been found in the Snowblind Bay formation on Cornwallis Island. Thorsteinsson correlated their horizon with late Silurian or earliest Devonian for structural reasons. However, the presence of *Pteraspis* as well as *Anglaspis* and *Ctenaspis* indicates a Dittonian age.

The occurrence in limestones and graptolitic shales in southeastern Yukon has been described by Hovdebo, Lenz, and Bamber (in Denison, 1963). The cyathaspid-bearing horizon is underlain by beds containing Early Wenlockian graptolites, and is overlain by beds with *Monograptus dubius;* the latter was believed to indicate that the age could not be younger than Middle Ludlovian. It has been shown recently (Jaeger, 1962, p. 112) that *M. dubius* ranges from the Late Llandoverian to the top of the Ludlovian. In view of this very long range, and of the fact that some species of *Monograptus* range well up into the Early Devonian (op. cit., table 3), it is possible that the Yukon fauna is considerably younger than Middle Ludlovian. It may well be Devonian, as is suggested by the presence of *Traquairaspis,* a genus that occurs typically in the Late Downtonian, and is found as high as the base of the Middle Dittonian (Ball and Dineley, 1961, table 1). *T. campbelli* is probably the earliest known member of the genus and may be of Early Downtonian age. The

Yukon fauna is now considered to be probably of Downtonian age, and is placed provisionally in the Early Downtonian.

A new locality, discovered in 1963 by California Standard Company geologists on the Snake River in northern Yukon, contains cf. *Dinaspidella* sp., Poraspidinae indet,. and Cyathaspidinae indet. These and the associated *Corvaspis* suggest an Early Devonian age. The vertebrates occur 40 to 50 feet above a limestone with brachiopods and corals of probable Late Silurian age.

Cyathaspididae have been found by California Standard Company geologists at two horizons on Mt. Sekwi, Northwest Territories, Canada. The lower horizon, designated 4994′–5080′, contains, besides *Vernonaspis sekwiae,* a coral and brachiopod fauna dated as Late Ludlovian by Alfred Lenz. The higher horizon, designated 4474′, contains only *Anglaspis expatriata.* The resemblance of this species to the British *A. macculloughi* is the basis for the correlation with Late Downtonian.

The new cyathaspids, *Listraspis* and *Pionaspis,* from northwest of Muncho Lake in British Columbia, were also collected by California Standard Company geologists, at a horizon designated 2100′. This horizon lies several hundred feet stratigraphically above Middle Silurian corals. The cyathaspids themselves are specialized and so suggest Devonian rather than Silurian age. With them is found a *Traquairaspis* of about the size of *T. symondsi,* and suggestive of a Late Downtonian age.

The fish-fauna of the Jones Creek formation of New Brunswick is difficult to date precisely. Its only cyathaspid is here referred to *Cyathaspis,* and appears to be close to *C. banksi,* which occurs in the latest Ludlovian and earliest Downtonian of Great Britain. The other vertebrates are coelolepids (*Thelodus*), a single presumed anaspid (*Ctenopleuron*), and acanthodian spines. Neither these nor the associated invertebrates, *Ceratiocaris, Bunodella,* and conodonts, are of much assistance in precise correlation of this formation. According to Arthur J. Boucot (in litt., Oct. 1, 1962) it is "most likely of Ludlow age," which conforms with the indication of the *Cyathaspis.*

The correlation of the Beartooth Butte and Water Canyon formations of Wyoming and Utah with the European section is based largely on the presence of *Protaspis* but is supported by the cyathaspids and arthrodires. These indicate a Late Dittonian or Early Siegenian age. The Holland Quarry Shale of Ohio is believed to be slightly older but still of Early Siegenian age (Denison, 1960, p. 609).

These formations contain the latest and largest known members of the Cyathaspididae.

In the northeastern United States a number of formations, mostly red beds, contain *Vernonaspis* and *Americaspis*. In only one case, the Vernon Shale of central New York, is there an associated invertebrate fauna, and in no case is there at present any very firm basis for correlation with the European section. All of the occurrences probably fall within the Cayugan Series, and it is probable that the boundary of this series with the underlying Niagaran is somewhere near the Ludlow-Wenlock boundary of England (Arthur J. Boucot, in litt., May 25, 1962). So the best that can be done at present is to place *Vernonaspis* and *Americaspis* somewhere within the Ludlovian.

## HABITAT

In a previous paper (Denison, 1956, pp. 371, 376–387, 416–417) I reviewed the habitat of early vertebrates and concluded that Silurian Heterostraci, all of which were Cyathaspididae, lived mostly in the seas. It was pointed out that while an isolated occurrence of a single cyathaspid might not be significant, a large number of such occurrences conforming to a pattern did have ecological significance. The absence of Heterostraci from presumed fresh-water or brackish Silurian vertebrate occurrences (Oesel $K_1$; Ringerike, Norway; and Lesmahagow inlier, Scotland) furnished additional, if negative, evidence in support of this hypothesis. Since the publication of the 1956 paper there have been new discoveries which strengthen this view.

The following Silurian and Early Downtonian cyathaspid occurrences are unquestionably marine:

| | |
|---|---|
| Late Ludlovian, England | *Cyathaspis* |
| Middle Ludlovian, England and Wales | *Archegonaspis* |
| Graptolithengestein, Germany and Poland | *Archegonaspis* |
| Hemse group, Gotland | *Archegonaspis* |
| Upper Oesel group ($K_4$), Oesel | *Tolypelepis* |
| Allen Bay formation, Cornwallis Island | *Tolypelepis* |
| Read Bay formation, Cornwallis Island | New cyathaspids |
| Cape Phillips formation, Cornwallis Island | *Tolypelepis* and new cyathaspid |
| Limestones and graptolitic shales<br>southeast Yukon | *Vernonaspis, Ptomaspis, Dikenaspis, Ariaspis, Homalaspidella* |
| Horizon 4994′—5080′, Mt. Sekwi<br>Northwest Territories | *Vernonaspis* |

The occurrence in southeastern Yukon is of special importance because the cyathaspids are both common and varied. They are found in dolomites in direct association with articulate brachiopods, fistuliporid bryozoans, and crinoids, and are in the midst of a series of shales that contain graptolites. The *Vernonaspis* from Northwest Territories is associated with a coral and brachiopod fauna.

The Jones Creek formation of New Brunswick is difficult to interpret ecologically. This occurrence, misidentified as the Long Reach formation by me (1956, p. 384), contains *Cyathaspis* associated with the coelolepid *Thelodus* and a few ceratiocarids. Other horizons contain acanthodian spines, conodonts, and abundant ceratiocarids. Unspecified horizons have yielded a single presumed anaspid (*Ctenopleuron*), and a xiphosuran (*Bunodella*), both suggestive of brackish or at least not typically marine conditions. The rock containing the *Cyathaspis* is very finely laminated, consisting of alternating thin dark carbonaceous shaly laminae, thin silts, and sometimes thicker clayey layers. All of these indicate quiet, perhaps sometimes stagnant waters. The mixed fauna is suggestive of marginal conditions, and lagoons come to mind as a possible site of deposition.

The other Silurian cyathaspid occurrences, with *Vernonaspis* and *Americaspis*, are in sequences of red beds in the northeastern United States. In many of these, the cyathaspids are the only known fossils. However, in the Vernon shale of central New York, *Vernonaspis* occurs in gray or buff shales intercalated in the red beds, and is associated with a varied invertebrate fauna much of which is undoubtedly marine. Fisher (1957, p. 21) concluded that the Vernon shale as a whole was deposited in "the littoral area of a restricted semi-marine environment," and that the faunal zone that contains the cyathaspids indicates a temporary marine invasion. The *Vernonaspis* of the Wills Creek formation of Maryland occurs in association with *Lingula* and ostracods (Leutze, 1960, p. 215), and is thus presumably brackish or marine. Fragments of Heterostraci, presumably cyathaspids, occur in the Bloomsburg formation of central Pennsylvania. The lithology and associated invertebrate fauna here indicate, according to F. M. Swartz (1946, p. 27) and Hoskins (1961, pp. 103–105), brackish waters in broad lagoons fed by a river system from the east. More eastern occurrences in the Bloomsburg formation of Pennsylvania, and the approximately equivalent High Falls formation of New Jersey, and Otisville shale member and Longwood shale of New York are considered to be probably fresh-water, alluvial deposits (Swartz, loc. cit.; Hoskins, loc. cit.; and Beerbower and Hait, 1959, p. 200). It should be noted, however, that the commonest fossil in these formations is *Vernonaspis*, which elsewhere is presumably an inhabitant of salt or brackish waters. In Perry County of central Pennsylvania the Wills Creek formation is topped by the Landisburg sandstone, in which *Americaspis* is common. The shales and limy beds in this formation contain abundant *Leperditia* and locally small brachiopods and gastropods, and so they are considered to be marine or brackish-water deposits. The Landisburg sandstone contains only *Americaspis* and is assumed by some to be a fresh-water deposit. Dr. James L. Dyson (in litt., June 29, 1963) notes characters of floodplain deposition, including obvious channels, associated with lagoonal features. He suggests that the environment was one mainly of small deltas in a lagoon. The position between marine beds of the underlying Wills Creek formation and the overlying Tonoloway formation indicate that this was deposited near the shoreline.

In summary, the Silurian habitat of most cyathaspids, even of some of those found in or associated with red beds, was clearly in the sea. Toward the end of the period, *Americaspis* and some *Vernonaspis* inhabited marginal habitats, perhaps both brackish and fresh-water.

Most Silurian cyathaspids belong to the Tolypelepidinae and Cyathaspidinae, few of which survive into the Devonian. The *Vernonaspis* from southeastern Yukon is now believed to be Early Downtonian and is marine. *Cyathaspis* occurs at the base of the Downtonian in the Downton Castle sandstone, which has been interpreted by me (1956, p. 391) and by Allen and Tarlo (1963, pp. 135–136) as a marine, probably brackish deposit, but was considered to be a fresh water or brackish deltaic deposit by Ball and Dineley (1961, p. 215). The Podolian genus, *Seretaspis*, probably comes from the Czortków stage, a shallow-water, marine deposit (Denison, 1956, p. 405). *Pionaspis* and *Listraspis* occur in deposits in which no associated invertebrates have been found, but the accompanying heterostracan, *Traquairaspis*, suggests a fresh-water habitat (op. cit., p. 417).

Most Early Devonian cyathaspids belong to the Poraspidinae, and with them are sometimes associated Irregulareaspidinae and Ctenaspidinae with probably similar habitats. With the exception of *Ariaspis*, *Homalaspidella*, and *Dikenaspis* from the Yukon, they are not found in typical marine deposits. They do occur often in marginal marine sediments, notably the Czortków stage of Podolia, many horizons of the Red Bay series of Spitsbergen, and the Water

Canyon formation of Utah (Denison, 1956, pp. 400–402, 405, 414). The Beartooth Butte formation at the type locality (op. cit., p. 414) and the Holland Quarry shale (Denison, 1960, pp. 610–611) were probably deposited in arms or estuaries of the sea where the waters may have been brackish or fresh. Other Early Devonian cyathaspid occurrences are in fresh-water deposits. Surely identifiable as such are the British Dittonian (Ball and Dineley, 1961, p. 217; Allen and Tarlo, 1963, pp. 143–146), and the Old Red of Podolia, both of which are probably deltaic. Probably fresh-water, but with intercalated marine beds, are much of the Late Downtonian of Britain, the beds with *Poraspis* in the Psammites de Liévin of France, and some horizons of the Red Bay series of Spitsbergen.

In summary, the early habitat of cyathaspids was in the seas. Their absence in most marine Silurian formations has been used by Romer (1946, p. 45) as an argument for a fresh-water habitat, but more probably indicates that they were largely restricted to some special marine ecological niches. That these were near-shore is suggested by the interpretations of many of the Silurian formations in which they are found. In the Late Silurian some cyathaspids show a trend into marginal habitats that may well have been brackish, and a few probably lived in fresh-water streams. This trend is continued in the Early Devonian, at which time almost all cyathaspids lived in marginal marine or fresh-water habitats.

## ADAPTATION

Cyathaspids have no close counterparts among living vertebrates, so it is difficult to determine their adaptation except in a general and sometimes speculative way. Most conclusions must be drawn from Kiaer's restoration based on the few articulated specimens of *Angaspis heintzi* (fig. 90).

The anterior part of the body was encased in a shield that was essentially immovable. The posterior part of the body, including the tail, was covered with overlapping scales, and so was flexible; but because the body scales were so large, the range and variety of movements must have been distinctly limited. There were no paired fins, and ridges and keels that would increase stability in swimming were often absent and rarely strongly developed. The body and tail probably formed a moderately powerful organ of propulsion. The tail itself, as restored by Kiaer, was somewhat asymmetrical and had an extended ventral lobe, stiffened by relatively large fulcral scales all around the margin. It is unlikely that strictly lateral movements in ordinary swimming would have resulted in elevating or depressing this tail to any great extent. With forward movement, lift would have been given to the anterior part of the body by the upwards slope toward the rostrum of the ventral surface. But progress in different vertical or lateral directions must have resulted largely from controlled movements of the body and tail. The swimming of cyathaspids may perhaps best be compared to that of tadpoles. They probably swam in any direction, with adequate control, quite rapidly for short spurts.

The following characters indicate that cyathaspids were not highly specialized for life on the bottom: their well-rounded contour, especially that of the strongly arched ventral shield; the lateral position of the eyes; the position of the mouth, which, though on the lower surface, must ordinarily have been some distance above the lowermost part of the body. It is probable, however, that cyathaspids spent much time on the bottom, at least when resting; this would have resulted from their presumed relatively high specific gravity, due to a heavy shield and probable lack of an air bladder.

The sensory equipment of cyathaspids included a pair of very small eyes that were directed laterally. The nostrils are believed to have opened into the anterior part of the roof of the mouth. It is possible that there were sensory barbels around the mouth, as suggested by Stensiö (1958, p. 355). Very probably the usual three pairs of semicircular canals were present. The lateral line system was strongly developed, and perhaps also the pore-canal system; this suggests that cyathaspids were well equipped for getting around in turbid or poorly lighted waters.

The manner of respiration of cyathaspids has been discussed above (p. 346). The main problem is the manner of production of a respiratory current, and it was concluded that there was probably a muscular pumping apparatus, perhaps derived from a velum.

For feeding, it is clear that there was no mechanism suited for biting or chewing. The oral plates, set in a skin membrane and worked by small muscles, served mainly to open and close the mouth. It is not unlikely that the mouth was protrusible, perhaps forming a scoop. With it cyathaspids could have scooped, sucked or perhaps even picked up detritus from the bottom, ingulfed small invertebrates, and swallowed small animals and plants that floated on or in the water. Much of their feeding may have been done on the bottom, but to accomplish this they would have had to elevate the tail and depress the snout.

## EVOLUTION AND GROWTH

The classical theory of the origin of dermal bones is credited largely to Hertwig (1876). He considered isolated placoid scales, such as occur in elasmobranchs, as primitive, and believed that dermal bones were formed by the enlargement and coalescence of the basal plates of such scales. This theory was applied to Heterostraci by Traquair (1899), who placed the Coelolepida, which have small, isolated scales, at the base of the phylogeny, and regarded the Psammosteidae and Pteraspididae (including the Cyathaspididae of the current classification) as successive stages in the fusion of the shield. There was wide acceptance of this concrescence theory.

In 1903 Jaekel pointed out that the paleontological evidence did not support the progressive fusion of plates, but suggested rather a phylogenetic subdivision of an originally continuous covering. Jaekel's brief statement was largely overlooked, and it was not until his theory was revived and developed by Stensiö (1927) that it became quite widely accepted by paleontologists. According to this theory, the Cyathaspididae, especially the Poraspidinae, were primitive, while the Pteraspididae, Psammosteidae, and perhaps Coelolepida, exemplified in that order the tendency toward subdivision of the shield.

In more recent years Obruchev (1945) has proposed another theory of the history of the heterostracan shield. He suggested that the primitive condition is shown by *Tolypelepis*, in which the shield appears to have been formed of a number of small plates or tesserae. *Cyathaspis* represents a later stage in which the tesserae have coalesced to form a shield of large plates. The pteraspids and psammosteids were derived from cyathaspids by subdivision of the shield into plates which could grow and so protect the animal not only as an adult, but also in its early stages. The Poraspidinae, on the other hand, were considered to be a side branch of cyathaspids in which the armor could not grow and appeared only after full size was attained. As far as this theory applies to the Cyathaspididae (though not to other families), it has been largely accepted and further developed by Stensiö (1958), Tarlo (1960, 1962a,b), and Ørvig (1961).

The paleontological evidence supports the view that a shield composed of many tesserae or scales was primitive in Heterostraci. The scale-units, of course, are relatively large, complicated structures, not the small, simple placoid scales considered primitive in Hertwig's theory. This was the type of shield possessed by the Ordovician genera, *Astraspis* and *Pycnaspis*. The earliest known cyathaspid, *Tolypelepis* (fig. 107), had a dorsal shield apparently composed in large part of scale-like elements. An early Downtonian cyathaspid, *Ptomaspis* (fig. 108), retained evidence of scale components in its dorsal shield. It has been assumed by Obruchev (1945, p. 264) and Stensiö (1958, p. 305) that the scale-like elements of *Tolypelepis* grew, and that they fused when adult size was attained. It can be shown that the individual tesserae of *Pycnaspis* did grow; thin sections demonstrate that small superficial tubercles were overgrown by larger tubercles of several generations, and concurrently new layers of aspidine were applied around the sides and base of the tesserae. Growth of the scale-units of *Tolypelepis* has not yet been demonstrated, and the descriptions of their growth by Stensiö (1958, pp. 297–306) are merely interpretations based on the dentine ridge pattern. Stensiö assumes that this genus had both "cyclomorial" scales that grew, and "synchronomorial" plates that formed all at once after the animal had attained full size. This seems most unlikely, especially as it is possible to interpret the "synchronomorial" areas (e.g., lateral and rostral epitega) as having grown also. There are three other possible interpretations of the *Tolypelepis* shield: (1) the apparent tessera, scale, and plate units of the dorsal shield all formed early in life and grew, fusing at maturity; (2) the subdivision of the dorsal shield was restricted to the superficial layer, and these superficial units may have grown, but the deeper layers did not develop until maturity; (3) there was no growth of the dorsal shield, all of which formed at maturity; in this case the scale-like units would be merely relics of the earlier evolutionary stage.

A more advanced evolutionary stage is exemplified by the Cyathaspidinae, in which the shield is formed of larger units, termed by Stensiö (1958, pp. 297, 308) "epitega" in the dorsal shield and "hypotega" in the ventral shield. Except in the posterior part of the dorsal shield of *Ptomaspis* and perhaps *Ariaspis*, there is no indication of scale-components that could have formed as separate units and fused at maturity.

It is necessary next to examine the nature of the units, epitega and hypotega. Kiaer (1932, p. 8) and White (1935, p. 437) considered the division of the shield to be merely superficial. But Kiaer and Heintz (1935, p. 40), Moy-Thomas (1939, p. 9), Obruchev (1945,

p. 265), and Stensiö (1958, p. 308) believed that in some genera at least, the epitega were distinct plates. The evidence now available does not lead to a definite answer. Epitega are already clearly marked in *Tolypelepis* (fig. 107). Precisely the same units are recognizable in Cyathaspidinae, where they are distinguished most clearly by the pattern of the dentine ridges. Thus in *Archegonaspis* (fig. 112,A), for example, the ridges of the rostral epitegum are largely transverse, those of the postrostral field radiate anteriorly, those of the central epitegum are approximately longitudinal, and those of the lateral epitega nearly parallel the lateral margins. These differences in pattern suggest that the superficial layer, at least, was formed in separate parts. Between the epitega there may be distinct external grooves that suggest sutures. However, sutures have not been demonstrated on the internal surface, nor are they apparent in thin sections (fig. 100,B). If epitega are formed as separate elements, one would expect to find them preserved separately, at least in an occasional juvenile individual. I know of no examples of this sort; in fact, the only specimen supporting the view that epitega are separate plates is the type of *Cyathaspis acadica* (fig. 111), where flattening during preservation has caused the dorsal shield to break into its rostral, lateral, and central epitega.

The manner of formation of the epitega has received relatively little attention. Could they have formed as scale-units that then fused together? This appears to be unlikely in Cyathaspidinae because there is usually no indication of such scale-units. In *Ptomaspis,* however, it is possible that the posterior part of the shield was formed in this fashion, though the anterior part probably was not. In those species of *Archegonaspis* and *Cyathaspis* that have dentine ridges of two sizes, it has been suggested by Obruchev (1945, p. 265) and Tarlo (1962a, p. 270) that the larger ridges belong to an earlier generation, and that the smaller ridges were formed later ontogenetically. This is almost certainly not the case. A thin section of one specimen of *Cyathaspis* cf. *acadica* (CNHM, PF 1800; fig. 159,A) reveals that the shield was in an early stage of formation and consisted only of a very thin capping of dentine on the ridges, continuing into a thin layer of aspidine around the intercostal grooves. The dentine is uniformly developed on all the ridges, high and low, and evidently had just been formed over much or all of the shield at the same time. This suggests that the shields of Cyathaspidinae formed only at mature size. The superficial layer developed first, and then presumably the deeper layers. The superficial layer may have been formed in units within the areas that are designated epitega, but this may not have been true for deeper layers. This manner of growth is very different from that of *Pycnaspis* and from that inferred by Stensiö for *Tolypelepis.*

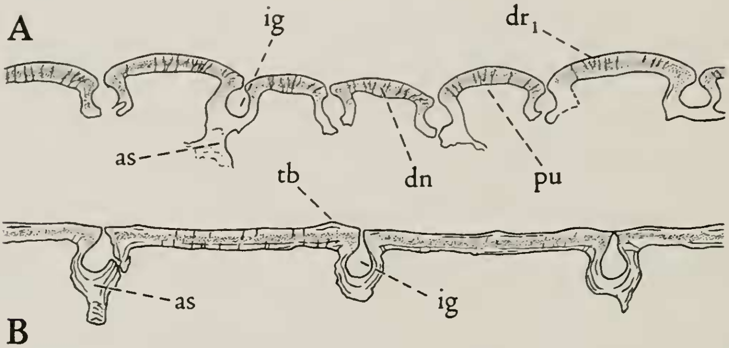


FIG. 159. Transverse sections of dermal shields of juvenile cyathaspids (× 75). A, *Cyathaspis* cf. *acadica*, CNHM, slide 4028; B, *Allocryptaspis laticostata*, CNHM, slide 4043.

*as*, aspidine; *dn*, dentine; $dr_1$, large elevated dentine ridge; *ig*, intercostal groove; *pu*, pulp cavity; *tb*, tubercle.

There is some question whether the ventral shield was subdivided into hypotega equivalent to the epitega of the dorsal shield. *Cyathaspis banksi* (fig. 110,B) has a band of fine ridges parallel to the anterior edge and to the anterior parts of the lateral edges; these were designated by Stensiö (1958, p. 308) "anterior postoral" and "marginal" hypotega. Similar bands are formed in *Cyathaspis acadica* (fig. 111) and in an undetermined cyathaspid from southeastern Yukon (Princeton 17094). But there are comparable ridges parallel to the anterior and lateral edges of both the dorsal and ventral shields of *Homalaspidella* (figs. 145, 147), a genus that has gone farther than any other cyathaspid in the reduction of epitega. This and the absence of any apparent subdivision of the ventral shield in most cyathaspids makes the presence of distinct hypotega seem improbable. The anterior and posterior "hypotega" that Stensiö (1958, p. 316) described in *Anglaspis insignis* have been shown above (p. 428) to be merely the result of an individual variation in ridge pattern.

Within the Cyathaspididae, the final evolutionary stage appears to be the loss of most or all traces of epitega. It is this feature especially that characterizes the Poraspidinae, and it is found also in the later genera of the Irregulareaspidinae. The significance of this change is clear: the dorsal shield, paired branchial plates, and ven-

FIG. 160. *Americaspis americana;* ventral shield, CNHM, PF 3308 (× 3/2), showing anomalous growth line (*gl*); photograph is of rubber impression of natural mold.

tral shield had become the main structural and growth units of the armor, and could have been formed only after growth had been completed. This is confirmed by a thin section of *Allocryptaspis laticostata* (fig. 159,B); though this specimen (CNHM, PF 3737) is of adult dimensions, its dorsal shield consists only of a very thin layer of dentine capping the ridges and continuing into a thin layer of aspidine surrounding the intercostal grooves. These thin layers are the earliest stage in the formation of the exoskeleton, and appear to have formed over the whole dorsal shield at once. The formation of the shield differs from that of the Cyathaspidinae only in that the superficial parts of the dorsal shield probably form as a unit rather than as separate epitega.

A few anomalies have some bearing on the formation of the cyathaspid shield. PF 3308, a ventral shield of *Americaspis americana*, has an irregular and somewhat asymmetrical, oval area in its center, marked by its ornamentation (fig. 160, *gl*). Within the area the ridges are mainly longitudinal, but curve near the anterior and posterior ends to run parallel to the periphery of the area. Outside the oval area, the ridges follow the usual irregularly longitudinal pattern, but near the oval area may curve to run parallel to its margin. The boundary of the oval area resembles a growth line, but in view of the conclusion that the shield of Poraspidinae did not grow, must have some other explanation. It is comparable to the "growth lines" of *Tremataspis* (Denison, 1947, pp. 362–365), and may be explained in a similar fashion, that is, as reflecting an anomaly in the development of superficial soft tissues previous to calcification of the shield.

Roughly comparable dentine ridge pattern anomalies subdivide the central epitegum of an undetermined cyathaspid from the Yukon (Denison, 1963, fig. 74) into: (a) a central area; (b) a postero-lateral area lying between (a) and the lateral epitegum, and forming the postbranchial lobe; and (c) a scale-like band along the posterior border. The subdivision of (a) and (b) is not shown in other cyathaspids and is of doubtful significance. The scale-like posterior band is known also in the dorsal shield of the type of *Ariaspis ornata* (fig. 148), where a distinct median scale is also included. It is entirely possible that the scales of these two specimens formed separately and then fused to the dorsal shield.

## PHYLOGENY

An attempt has been made in figure 161 to show the phylogeny of the Cyathaspididae, although it is necessarily generalized and provisional. The major phyletic subdivisions are here considered to be subfamilies, but within each subfamily details of phylogenetic history are rarely determinable. The Tolypelepidinae are believed to include the ancestral stock of the family. From them was derived the Cyathaspidinae by loss of scale-components in the shield. In this subfamily *Ptomaspis* is the most primitive genus; from some such form could well have been derived the closely related and rather unspecialized *Archegonaspis*, *Vernonaspis*, and probably *Seretaspis*. *Cyathaspis* occupies a more isolated position within the subfamily, and this is also true of the late and specialized *Pionaspis* and *Listraspis*. The Irregulareaspidinae are a distinctive branch, probably derived from early Cyathaspidinae. The Early Downtonian *Diken-*

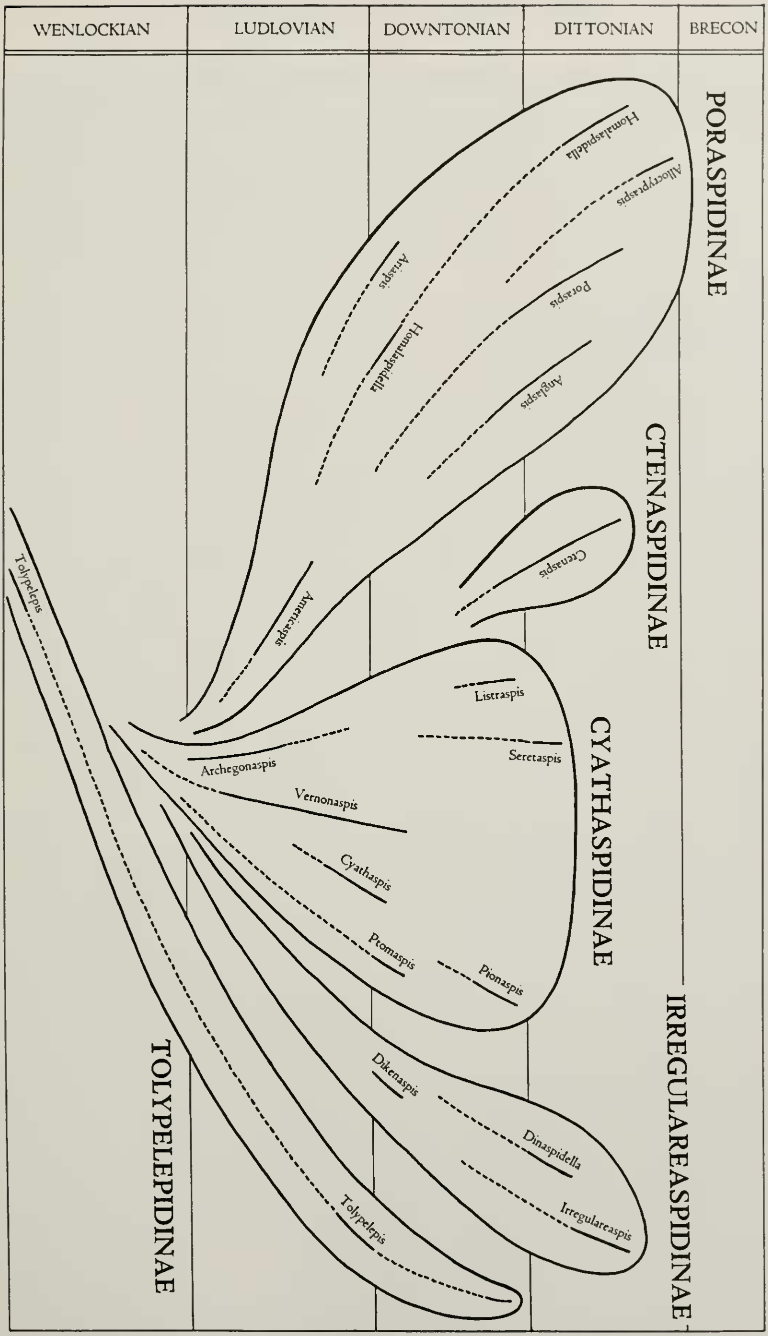


Fig. 161. Phylogeny of the Cyathaspididae.

*aspis* retains epitega, but these are reduced or lost in the later genera. The Poraspidinae may represent an artificial assemblage of genera that have independently lost distinct epitega. The Silurian *Americaspis,* though possibly not directly ancestral, could be close to the stock from which *Poraspis* was derived. *Allocryptaspis* could easily have been derived from this same stock. The European *Homalaspidella* is probably derived from the *Poraspis* stock, but the Canadian species could represent a distinct but parallel line. *Ariaspis* and *Anglaspis* are quite isolated within the subfamily. The most distinctive cyathaspids, the Ctenaspidinae, are of obscure ancestry. The absence of any apparent division of their dorsal shield into epitega has suggested relationship to the Poraspidinae (Kiaer, 1930, p. 5), but more probably results simply from the loss of the superficial layer. As far as present information shows, *Ctenaspis* could have been derived from either the Poraspidinae or Cyathaspidinae. It is unlikely that it evolved entirely independently from other cyathaspids, as Zych (1931, p. 87) and Stensiö (1958, p. 319) concluded.

None of the subfamilies of Cyathaspididae are known to have survived the Early Devonian, and the question arises as to whether these phyletic lines all became extinct without leaving any descendants. Those who have supported the theory of progressive phylogenetic subdivision of the heterostracan shield (p. 457) have believed in general that the Poraspidinae, Cyathaspidinae, Pteraspididae, and Psammosteidae, in that order, represent morphological if not evolutionary stages. Obruchev (1945, p. 265) presented an improvement on this theory according to which such a form as *Cyathaspis* gave rise on the one hand to the Poraspidinae, a side branch that died out early, and on the other hand to the Pteraspididae and through them to the Psammosteidae. Stensiö (1958, p. 252), following his lepidomorial theory, has explained the differences between the families as the result of fusions of smaller or larger elements. The cyathaspids were considered by him to be more advanced than the pteraspids because of greater fusion, and the ancestors of the pteraspids were believed to be forms like the psammosteids with belts of smaller scales separating the larger plates. Tarlo (1962a, p. 272) has followed this view. This is not the place to enter upon detailed criticism of the lepidomorial theory, but one point needs to be emphasized. It is probable that many evolutionary changes, including some within the Heterostraci, have resulted from fusions of smaller skeletal elements to form larger elements. It is also probable in other cases that evolution has resulted in the subdivision of larger elements to form a few or many smaller elements. One cannot, therefore, automatically gauge the evolutionary advancement within the Heterostraci by the degree to which fusion of the shield has progressed. Specifically, one cannot exclude the possibility of derivation of pteraspids from cyathaspids because subdivision of the shield is involved. There are a number of arguments in favor of a derivation of pteraspids from the Cyathaspidinae; they are:

1. The known geological ranges of the Cyathaspidinae and Pteraspididae favor it. The former range from Early Ludlovian into Early Dittonian. The latter first appear in Late Downtonian, near the end of the range of the Cyathaspidinae.

2. The epitega, branchial plates, and ventral shield of Cyathaspidinae are comparable to the plates of the pteraspid shield. The pineal plate of the latter may have arisen from a new center of ossification in the postrostral field of cyathaspids. Derivation of the pteraspid orbital plate, which surrounds the eyes, from the cyathaspid lateral epitegum, which is only notched for the eye, presents no real problem. It could have been accomplished either by a growth of the lateral epitegum down and around the orbit, or by fusion of the suborbital plate to the lateral epitegum. The dorsal spine of pteraspids was derived from a scale that attached to the dorsal shield, as has clearly happened in *Ariaspis ornata* (fig. 148) and *Pteraspis carmani* (Denison, 1960, p. 578). The cornual plates of pteraspids could have evolved from a pair of scales that attached to the postero-lateral corners of the dorsal shield.

3. The pteraspid lateral line pattern is easily derivable by minor modifications of the simple pattern of cyathaspids.

4. A thin section of a juvenile *Protaspis* (CNHM, slide 4070) shows that a very early stage of formation of a dorsal disc, approximately 12.5 mm. long, is similar to an early stage of the shield of *Cyathaspis* (fig. 159,A) or *Allocryptaspis* (fig. 159,B). A thin layer of dentine caps the ridges and is joined by a thin layer of aspidine around the intercostal grooves, the whole developing at one time over the juvenile disc. Later, presumably, the reticular, cancellous, and basal layers are formed. The essential difference in the pteraspids is that following this early stage, the dorsal disc and other plates do not fuse as they do in cyathaspids, but are added to by successive peripheral growth increments until adult size is attained.

5. Certain cyathaspids approach pteraspids in one character or another. Some cyathaspids have a dentine ridge pattern close to that of pteraspids, transverse on the rostrum and broadly elliptical on the

central epitegum and ventral shield. A ridge scale is attached to the central epitegum of *Ariaspis*, homologous to the pteraspid dorsal spine. The suborbital plate of *Listraspis* is fused to the lateral epitegum, completing the encirclement of the orbit. The narrow-crested, crenulated ridges of *Listraspis* are similar to those of pteraspids.

These points favor the belief that the pteraspids were derived from cyathaspids. The most important advance in pteraspids was the mechanism permitting growth of the shield. This made it possible for the shield to form early, thus protecting the larval pteraspid, yet permitting growth sometimes to a considerable size (White, 1958, pp. 229–232). The acquisition of dorsal spine and cornual plates by pteraspids must have given them somewhat more stability in swimming, but these adaptations sometimes appear in cyathaspids, though usually in a different way. The scales of the posterior part of the body are relatively smaller in pteraspids than in cyathaspids, permitting greater flexibility. The development of an enlarged rostrum on many pteraspids would give added lift in swimming to the anterior part of the body. These points all indicate that some pteraspids were better swimmers than cyathaspids, though, since no paired fins were evolved, their ability was limited.

There is no strong evidence for the derivation of other families of Heterostraci from cyathaspids. Obruchev (1945, p. 265) believed that the Psammosteidae were derived from Pteraspididae, and thus more remotely from Cyathaspididae. Stensiö (1958, p. 334) thought that *Cardipeltis* was derived from primitive cyathaspids, but its relationship to the latter is unlikely. There is, at present, no very close approach between Cyathaspididae and Traquairaspididae.

## SUMMARY

The Cyathaspididae, a family of Agnatha from the Silurian and Early Devonian, are considered from many points of view. The structure of their dermal skeleton is described, including a comprehensive account of its histology. The evidences for internal structure are discussed, and the reconstructions by Stensiö of the internal anatomy are criticized. It is concluded that the order Heterostraci, to which Cyathaspididae belong, is a very primitive group of vertebrates, not closely related to modern cyclostomes, or to fossil Osteostraci and Anaspida.

The systematic revision is concerned primarily with North American forms, but all genera and species are included. The family is divided into the following subfamilies and genera:

Tolypelepidinae: *Tolypelepis.*

Cyathaspidinae: *Ptomaspis, Cyathaspis, Archegonaspis, Seretaspis, Vernonaspis, Pionaspis* (gen. nov.), and *Listraspis* (gen. nov.).

Irregulareaspidinae: *Dikenaspis, Dinaspidella,* and *Irregulareaspis.*

Poraspidinae: *Poraspis, Americaspis, Homalaspidella, Ariaspis, Anglaspis,* and *Allocryptaspis.*

Ctenaspidinae: *Ctenaspis.*

The following generic revisions are made: *Diplaspis acadica* (Matthew) is referred to *Cyathaspis; Cyathaspis vaningeni* Bryant is referred to *Vernonaspis; Aequiarchegonaspis* Stensiö and *Lauaspis* Stensiö are referred to *Archegonaspis; Fraenkelaspis* Stensiö is referred to *Anglaspis.*

The following new species are described: *Vernonaspis bryanti* from the Late Silurian of New Jersey, New York and Pennsylvania; *V. sekwiae* from the Late Silurian, and *Anglaspis expatriata* from the Early Devonian of Northwest Territories, Canada; *Pionaspis planicosta, P. acuticosta,* and *Listraspis canadensis* from the Early Devonian of British Columbia; and *Americaspis claypolei* from the Late Silurian of New York.

The geologic age of the various cyathaspid occurrences is considered and displayed in a correlation chart. Their habitat is shown to have been first in the seas, though many later species lived in marginal, often brackish habitats, and in fresh-water streams. The locomotor, sensory, respiratory, and feeding adaptations are discussed.

In the evolution of the family, the primitive condition is believed to be a shield formed by the fusion of numerous small tesserae. In later forms the shield is composed of large plates, formed only when the animal had reached full size. The derivation of Pteraspididae from Cyathaspididae is defended, and involves the subdivision of the shield into plates that can form early and grow with the animal.

The subfamilies of Cyathaspididae are believed for the most part to be distinct phyletic lines, with the Tolypelepidinae including the ancestral stock, the Cyathaspidinae representing a central line leading to pteraspids, and the other subfamilies diversely specialized side lines.

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